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Larval Fish Recruitment and Research in the Americas

Thirteenth Annual Larval Fish Conference
Mérida, México, May 1989

Robert D. Hoyt (editor)

U.S. Department of Commerce

NOAA Technical Report NMFS

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Larval Fish Recruitment and Research in the Americas

Proceedings of the Thirteenth Annual Larval Fish Conference
Mérida, México
21–26 May 1989

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Sponsored by:

Mote Marine Laboratory and
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January 1991

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CONTENTS

PREFACE iv

KEYNOTE ADDRESS

J.D. de CIECHOMSKI — A review of investigations on early developmental stages and larval recruitment of marine fishes in South America — 1

REPRODUCTION AND BIOMASS ESTIMATION

B.H. COMYNS, J. LYCZKOWSKI-SHULTZ, D.L. NIELAND, C.A. WILSON — Reproduction of red drum, *Scienops ocellatus*, in the north-central Gulf of Mexico: seasonality and spawning biomass — 17

A. RAMÍREZ-ESTÉVEZ, M. ORNELAS-ROA — Larval distribution and abundance of the Scombridae in Campeche Sound, with emphasis on the frigate tunas (*Auxis* spp.) — 27

DISTRIBUTION AND ABUNDANCE

J.H. MUELBERT, G. WEISS — Abundance and distribution of fish larvae in the channel area of the Patos Lagoon Estuary, Brazil — 43

C. FLORES-COTO, U. ORDOÑEZ-LÓPEZ — Larval distribution and abundance of Myctophidae, Gonostomatidae, and Sternoptychidae from the southern Gulf of Mexico (1983–1984) — 55

LARVAL TRANSPORT AND MIGRATION

J.J. LOOS, E.S. PERRY — Larval migration and mortality rates of bay anchovy in the Patuxent River — 65

B.L. NORCROSS, D.A. BODOLUS — Hypothetical northern spawning limit and larval transport of spot — 77

MICROHABITAT SELECTION

G.D. DENNIS, D. GOULET, J.R. ROOKER — Ichthyoplankton assemblages sampled by night lighting in nearshore habitats of southwestern Puerto Rico — 89

J.B. LAYZER, M.D. CLADY — Microhabitat and diet segregation among coexisting young-of-year sunfishes (Centrarchidae) — 99

TAXONOMY AND MORPHOLOGY

J.A. CAMBRAY — Comparative Scanning Electron Microscopy studies of the egg envelopes of six African *Barbus* and three *Pseudobarbus* species (Cyprinidae) — 109

M.F. DeLEON, R.O. REESE, W.J. CONLEY — Effects of fixation and dehydration on shrinkage and morphology in common snook yolk-sac larvae — 121

R.O. REESE, M.F. DeLEON, W.J. CONLEY — Histological effects from long-term storage of common snook yolk-sac larvae in fixatives and alcohol — 129

PREFACE

The 13th Annual Larval Fish Conference and Annual Meeting of the American Fisheries Society Early Life History Section cohosted by Mote Marine Laboratory, United States, and the Instituto Nacional de la Pesca, Mexico, were held 21–26 May 1989, in Mérida, Yucatán, México. The purpose of holding the meeting in Mexico was to encourage the participation of our Latin American and Caribbean colleagues and to provide a forum for the exchange of ideas and information among researchers working in the Americas. More than 150 participants represented 24 U.S. states, the District of Columbia, and 13 foreign countries including Mexico, Canada, Puerto Rico, Costa Rico, Panama, Cuba, Columbia, Chile, Peru, Brazil, Argentina, South Africa, and West Germany.

The Conference began with registration and a social in the courtyard patio of the Mérida Holiday Inn. Fresh red grouper, the most important commercial finfish species of the State of Yucatán, was prepared and served by the hotel staff, courtesy of CPI, Itzamex, and the Terramar Trading Company.

Plenary sessions opened and closed the Conference. The first plenary session opened with a welcome from Ing. Carlos Rihani, the Federal and State Fisheries Delegate who represented Lic. Victor Manzanilla, the Governor of the State of Yucatán. Also adding a few welcoming remarks were Lic. Raúl Diego, Director of the Centro Regional de Investigación Pesquera Yucalpetén (Instituto Nacional de la Pesca), and Robert Werner, the AFS Early Life History Section President. Following the welcome, Cuban representative Biologist Maida Montolio presented a short tribute to the memory of Mar Júarez, the pioneer of ichthyoplankton research in Cuba, who died shortly before the Conference.

Four speakers delivered keynote addresses on the theme of the Conference, "Larval Fish Recruitment and Research in the Americas": William Richards, National Marine Fisheries Service–Miami (North America); Biologist Rosa Maria Olvera, Instituto Nacional de la Pesca, Mexico City (Mexico and Central America); Douglas Shapiro, University of Puerto Rico (Caribbean); and Juana D. de Ciechomski, Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina (South America), all of whom provided a synopsis of the major areas of larval fish research being conducted in the geographic regions they represented. Juana D. de Ciechomski's paper entitled, "A Review of the Investigations on Early Developmental Stages and Larval Recruitment of Marine Fishes in South America," appears in this volume.

Following the first plenary session, four days of concurrent sessions covered the topics of migration and dispersal, taxonomy, recruitment, feeding ecology, reproductive strategies, ecology, fish culture, physiology, biochemistry and behavior, and a special scombrid session. A poster session and three major workshops were held during the Conference. William Richards conducted the Scombrid Workshop; Darrel Snyder the Taxonomy Workshop; and Stanley Warlan, Perce Powles, and J. Isley the Age and Growth Workshop. Also included were VCR presentations, exhibits by publishers and manufacturers and a special exhibit of larval fish reference literature compiled by Darrel Snyder valued at over $2,000 and which was donated to the Instituto Nacional de la Pesca following the Conference. A total of twenty posters and eighty-nine oral papers were presented. Of the eighty-nine presentations given, twelve are published in this volume. Exclusing the keynote address of Juana D. de Ciechomski, they are organized into Reproduction and Biomass Estimation, Distribution and Abundance, Larval Transport and Migration, Microhabitat Selection, and Taxonomy and Morphology sections. Unlike other conference editions, the

topics in this symposium are diverse. As such, they are truly representative of the 13th Annual Larval Fish Conference which was in itself a break with tradition, overcoming language barriers and geographic boundaries—an example that diversity can provide the strength for unity.

There were ten candidates for the annual Sally Richardson Best Student Paper Award. The panel of judges, Grace Klein-MacPhee, University of Rhode Island, USA; Scott Holt, University of Texas, USA; Jeffrey Marliave, Vancouver Aquarium, Canada; and Yasunobu Matsuura, Instituto Oceanographico da Universidade de Sao Paulo, Brazil, presented the award to co-recipients David M. Goshorn (University of Delaware) for his paper, "The Diet of Larval Weakfish, *Cynoscion regalis*, in Delaware Bay and the Relationship of Prey Density to Larval Growth and Survival," and a Columbian student, Guillermo Moreno (Moss Landing Marine Laboratory, California) for the paper "Descriptions of the Early Rockfishes (*Sebastes* spp.) from Central California."

During the final plenary session there was an evaluation of the Conference goals and suggestions for continuing and enhancing international growth within the Early Life History Section.

A field trip was made to the Mayan ruins in Uxmal and a diving trip to the reefs off Cozumel. The Conference ended with a fiesta at a Mexican hacienda. Typical Yucatecan dishes were served while strolling mariachis serenaded banquet attendees.

As Conference Chairperson, I would like to thank Andrea Frank, my Assistant Coordinator, without whose help there would not have been a Conference. I also wish to thank other Mote Marine Laboratory personnel: Linda Franklin, Marilee Lipinski, and Robert Dixon; and NMFS personnel, William Richards and Nikki Bane, for their dedicated work on behalf of the Conference. I am indebted to Roberto Freund who translated all the Conference abstracts and Roberto Donadi of Recursos Técnicos para Conferencias, S.C., for the excellent simultaneous translations. I also wish to thank Fred Binkowski for all his help in disseminating conference information in the Early Life History Section Newsletter. A special thank you is also in order for Conference sponsors NOAA/National Marine Fisheries Service Southeast Fisheries Center, United Nations Environment Programme, CPI, Itzamex, Terramar Trading Company, Mexicana Airlines, Collezio National de Educación Profesional Tecnica, and the Department of Tourism of the State of Yucatán. Finally, I would like to thank all those who attended and gave presentations.

All participants of the 13th Annual Larval Fish Conference were invited to submit their papers in English for this publication. Because English is a foreign language for many of the authors and international mail service can be slow and unpredictable, an extra burden was placed on many authors and especially on the reviewers. A total of thirty-three peer reviewers were involved in the review process, and their expertise and assistance in bringing this work to fruitation are sincerely appreciated. I would like to thank AFS/ELHS Editor Robert Hoyt and his Associate Editors, Dannie Hensley, Douglas Markle, John Olney, Robert Olson, Eileen Setzler-Hamilton, and William Szelistowski for their patience, perseverance, and commitment to producing this special symposium edition. For their Herculean efforts, this publication is dedicted to them.

Karen M. Burns
Conference Chairperson
Mote Marine Laboratory
Sarasota, Florida

A Review of Investigations on Early Developmental Stages and Larval Recruitment of Marine Fishes in South America

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ABSTRACT

This paper presents a summary of studies on eggs, larvae, and juveniles of marine fishes in South America, with an emphasis on recruitment. A brief review is given of the history of these studies in different countries. The countries included are on the Pacific coast: Peru, Chile, Ecuador, Colombia; the Atlantic coast: Argentina, Uruguay, Brazil; and the Caribbean coast: Venezuela.

Introduction

The purpose of this paper is to summarize research on early developmental stages of marine fishes and their recruitment recently carried out in South America (Fig. 1). This summary intends to point out various lines of research that have developed. Continued updating of our knowledge in this field will lead to improved research.

When one analyzes the evolution of these studies in South American countries, it becomes clear that South American advancements parallel advancements at a worldwide level. As in other parts of the world, scientists and managers realize that studies related to early developmental stages of fish can provide basic data for estimation both of biomass of spawning stocks and of future recruitment. This is especially evident in pelagic species that usually have a short lifespan, are directly dependent on the environment, and are subject to marked fluctuations in their populations. It has been generally accepted that fluctuations in recruitment represent one of the major causes of changes in abundance of fish populations under exploitation, and that the mechanisms determining the magnitude of recruitment depend not only on the production of eggs and larvae but also on their environmentally induced mortality (predation, starvation, advection). During the last decade in South America, oceanographers have worked with fishery biologists to improve understanding of this complex problem.

Studies related to early life history of marine fish in South America have gone from a descriptive stage, which existed in some countries in the 1950's, to a stage where investigations focus on national management of fishery resources. All of these studies began first in countries with economies heavily influenced by fishing activities, such as Chile and Peru. These countries border one of the richest current systems in the Eastern Pacific, the hydrographic characteristics of which assure high productivity (Parrish et al. 1983). This fact, together with world interest in the region, resulted in collaboration involving developed countries and international organizations that brought together scientists and funds to carry out programs that could not have been performed entirely within a single country.

An analysis of early life history and recruitment studies in each country, together with a summary of present knowledge, is presented in this paper.

Pacific Coast

Peru

The development of research related to early life history of fish in this country was directly related to the hydrobiological regime off Peru. Because of intense and permanent upwelling, the Peru off-shore area is one of the most productive in the world. The intense upwelling and cyclical perturbations, caused by the El Niño phenomenon, support its high productivity. Several major currents, directed towards the South Pole as well as the Equator, determine temperature, oxygen, and nutrient regimes. This habitat supports an important community of pelagic fishes that has a large biomass and few species. Marked fluctuations in stocks are observed. The most important exploited species are the anchovy *Engraulis ringens*, the sardine *Sardinops sagax*, the jack mackerel *Trachurus murphi*, and the mackerel *Scomber japonicus*.

* Miembro de la Carrera del Investigador Científico y Tecnológico, Consejo Nacional de Investigaciones Científicas y Técnicas.

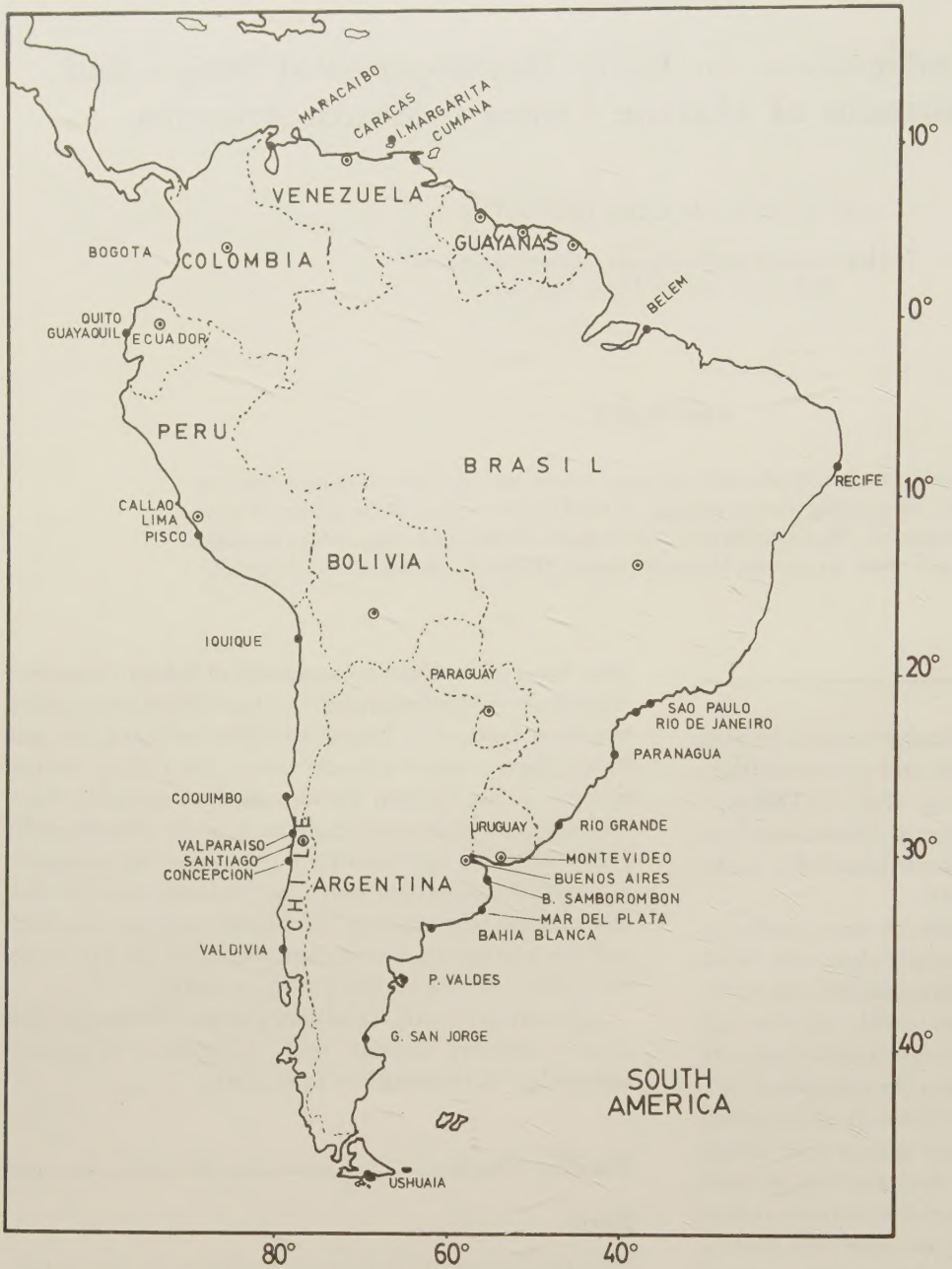

Figure 1
Location of main South American Laboratories where early life-history studies of fish are being carried out.

In the 1950's and 1960's, several papers were published in Peru on reproduction, morphology and distribution of fish eggs and larvae. In the 1960's, the research effort was directed toward the anchovy fishery which became the largest in the world, reaching 12.3 million metric tons in 1970.

Studies of ichthyoplankton and anchovy sexual maturity indicate that the spawning period for anchovy lasts 8 to 9 months, from July to March, with the highest intensity between August and September (Tsukuyama 1983). The most important area for spawning is located off-shore of the northern central Peruvian coast between lat. 06° S and 14° S. This is positively correlated with phytoplankton abundance (Rojas de Mendiola and Ochoa-Lopez 1980; Santander 1980).

Owing to intense fishing effort and environmental changes caused by "El Niño," as in 1972, anchovy biomass began to decline and other pelagic species such as the sardine, jackmackerel, and mackerel gained importance as fishery resources. The scientists of the Instituto del Mar del Peru (IMARPE) began to study other species and intensified their investigations on mechanisms which are related to fluctuations of pelagic resources and the interactions of several elements within the ecosystem.

The drastic fall of the anchovy fisheries in Peru moved many countries and international organizations, such as

FAO and UNESCO (IOC), to offer help (Dickie and Valdivia 1981). By the end of 1976, a cooperative agreement was signed between Peru and Canada and a Cooperative Research Program on the anchovy and its ecosystem (ICANE) began with the collaboration of IMARPE and several Canadian institutions. Scientists of other countries, mainly from the United States, also participated.

Later, a Peruvian–German Cooperation Program was signed (PROCOPA) involving the Technical Cooperation German Agency (GTZ) and IMARPE. Participants included W. Arntz and J. Albeit from Germany, as well as scientists from other countries and international organizations such as: A. Bakun, R. Parrish from SWFC, P. Smith, S.R. Goldberg, and B.J. Macewicz; D. Pauly from International Living Resources; and J. Csirke from FAO. All foreign groups closely collaborated with local scientists from IMARPE. Multidiscipline research efforts were the specific focus of the program. Recently, Peru has made plans to enter the yet to be implemented Sardine and Anchovy Recruitment Program (SARP).

Many papers resulting from these collaborations are included in three large volumes: 1) "Investigación cooperativa de la anchoveta y su ecosistema entre Perú y Canadá" (Bolet. Vol. extraord., Inst. del Mar del Peru, Callao, Peru, 1981; 2) "El Niño, su impacto en la fauna marina" (W. Arntz, A. Landa, J. Tarasona, eds.), IMARPE, vol. extr., 1985 (together with GTZ); and 3) "The Peruvian anchoveta and its upwelling ecosystem: three decades of change" (D. Pauly and I. Tsukayama, eds.), ICLARM Studies and Reviews 15. Many of these papers concern recruitment as related to parental stock, as well as to physical-oceanographic phenomena.

An important methodological paper is that of Santander et al. (1982) in which the sampling effort required for determining egg-production estimates for anchovy was developed. Santander (1987) analyzed the relationship between egg abundance and biomass of spawning stock of anchovy and found high cannibalism by adults on their own eggs. The same phenomenon was corroborated by Santander et al. (1983) and Santander and Alheit (1984), who noted that the main causes for embryonic mortality of anchovy were cannibalism and predation by sardine.

Parrish et al. (1981), working on the relationship between transport mechanisms and fish reproduction in the California Current, have provided interesting observations on anchovy reproduction in the Peruvian current system (Bakun and Parrish 1982). They pointed out that the spawning peak for anchovy occurs during winter, when the Ekman transport from the coast to off-shore areas is more intense, contradicting the currently accepted theory.

Pauly and Tsukayama (1987) and Mendelsohn and Mendo (1987) should also be noted in relation to anchovy recruitment. Pauly and Soriano (1987) analyzed anchovy monthly egg production between 1953 and 1981 and noted that production peaks did not coincide with the peaks of the next recruitment, results similar to the observations of Mendelsohn and Mendo (1987). The latter authors suggest that it is possible to predict trends of future recruitment, information required for better management of anchovy stocks.

Santander and Flores (1983) studied egg and larval distribution of anchovy, sardine, jack mackerel, and mackerel in relation to temperature, salinity, coastal blooming, superficial currents, and "El Niño" from 1964 to 1982. Also of interest are studies by Castillo (1985) on variations of ichthyoplankton distribution and Carrasco (1988) on myctophid larval abundance in the Peruvian Sea.

Muck et al. (1987) discussed the relationships between the abundance of sardine, mackerel, and jack mackerel eggs and larvae and temperature, turbulence, and anchovy biomass. The studies of Espino and Wosnitza Mendo (1984) on the stock-recruitment relationship of the hake *Merluccius gayi peruanus* indicated that a Ricker-type curve may be applied, where stock and recruitment are inversely related. They found that in 1982 the number of recruits was at a low level and therefore recommended conservative management of the stock for 1983.

In 1981 the egg production method for assessing the biomass of spawning anchovy (Alheit et al. 1983; Santander et al. 1984) was first used in Peru. This method was developed by Hunter and Goldberg (1980) and Hunter and Macewicz (1980). In a related area, studies on fecundity and spawning frequency were carried out by Alarcón and Alheit (1984), Alegre and Alheit (1984), Alheit et al. (1984), Alheit (1985), and Lo et al. (1986) on sardine and Peña et al. (1986) on mackerel.

Research on anchovy larval feeding started by the end of the 1960's and has continued to the present. Some papers published in the 1980's include observations on maintenance ration, growth efficiency, and food density for the maintenance of anchovy and sardine larvae (Rojas de Mendiola and Gomez 1980, 1981; Ware et al. 1981; Villavicencio 1981; Villavicencio and Muck 1983). A study by Walsh et al. (1980) considered anchovy larval feeding in association with mortality and recruitment in the natural environment, including during an "El Niño". Villavicencio and Muck's (1985) work on minimum vital density of food for anchovy and sardine larvae based on a growth and feeding model is important. The same authors also discussed the negative influence of high temperatures on survival and development of embryos and larvae of both species. Additional studies are now being carried out on starvation in pelagic fish larvae. Recently, studies on age and daily growth of anchovy larvae have been initiated using daily rings in otoliths (Palomares et al. 1987). Another research effort presently being carried out in IMARPE is that related to Bothidae larvae by Girón.

IMARPE is the institution where the majority of early life-history studies are performed. Its scientists include S. Carrasco Barrera, O.S. de Castillo, M. Espino,

M. Girón, D. Gomes Caballero, O. Lotzano Rubio, J. Mendo, P. Muck, N. Ochoa Lopes, J. Tsukayama, Z. Villavicencio, C. Wosnitza-Mendo, and S. Zuta. In addition there is interest from some scientists from the Universities of Lima, Callao and Trujillo. Finally, Haydée Santander of IMARPE, who died in 1987, should be mentioned here because she obtained inestimable success in this field.

Chile

The oceanographic conditions along Chile's coast correspond, as in Peru, to the eastern ocean currents. The area is characterized by high productivity, intense upwelling, and changes in oceanographic conditions caused by the cyclic phenomenon "El Niño." The hydrological characteristics are determined mainly by the influence of the Humboldt Current moving toward the Equator at a distance of 100 to 200 miles from shore. Inshore there is a poleward current called the Peru–Chile Countercurrent. Also, there are subsurface flows, with wind-driven flows predominating at the surface.

In this unstable habitat, several fish species reside, the pelagic ones being the most important. They are: the anchovy *Engraulis ringens*, the Spanish sardine *Sardinops sagax*, the jack mackerel *Scomber japonicus*, and the common sardine *Clupea = Strangomera bentincki*. Interspecific interactions among the populations have subjected the species to many changes, particularly in connection with their abundance, geographic distribution, and spawning areas. The most spectacular recent events were the collapse of the anchovy and the "explosion" of the Spanish sardine. It has been determined that while the anchovy and Spanish sardine concentrate in definite spawning areas producing high egg densities, the jack mackerel spawns in larger areas with fewer eggs (Serra 1983).

Because of the importance of pelagic fisheries (approximately 80% of the total), the great majority of studies on reproduction and recruitment have been directed at these species. The first investigations were descriptive works on morphology and identification. They continue at present, the most recent including a comparative study of Clupeiformes in the Chilean coasts by Orellana and Balbontin (1983); Martínez et al. (1983) on *Scomberesox saurus scombroides*; Balbontin and Orellana (1983); Palma et al. (1985) and Acuña (1986, a and b) on myctophids; Herrera (1984) on blennids, Nelson et al. (1985) on *Psychrolutes*; Mujica (1988) on the jack mackerel; Rojas (1988) on the sardine and anchovy; Silva (1988) on flatfish *P. adspersus*; and Muñoz et al. (1983) on *Paralichthys microps*. Recent work dealing with ichthyoplankton in general include those of Palma Fuenzalida (1985), Aron (1986), Palma and Pizarro (1987), Palma (1988), Castillo et al. (1983), and of Loeb and Rojas (1988) on inter-annual variations between 1964 and 1983.

Some investigations on distribution and abundance of fish eggs with other biological parameters have been performed in order to assess the biomass of sardine and anchovy spawning stocks. After the collapse of its anchovy fishery, efforts since 1972 have been mainly concentrated on species that increased in abundance, particularly the sardine. Also, studies on other aspects of early life history of fish, particularly related to larval survival and recruitment have been undertaken.

Studies have been carried out on feeding, both at sea and in the laboratory, and include that by Herrera and Balbontin (1983) on intestinal evacuation rates and the incidence of feeding in Spanish sardine larvae. Garretón (1983) reported on the bio-energetics of yolk utilization in embryos and vitelline larvae of *Hypomesus pretiosus* and Balbontin et al. (1986) on food conposition, and size of prey in fish larvae of the Bransfield Strait (SIBEX) in the Antarctic. Uriarte and Balbontin (1987) studied starvation of Spanish sardine larvae, using morphometric and histological methods.

Together with studies on food and feeding habits, investigations on growth of fish larvae were undertaken using daily otolith rings on Spanish sardine (Garretón and Balbontin 1982; Castillo et al. 1985; Balbontin and Cannobio 1988; Garland 1988) and on Spanish sardine and anchovy (Herrera et al. 1985; Herrera et al., in press, a and b).

Studies have also been performed on parasitism in fish larvae by Herrera (1984, in press). At the Pontificia Universidad Católica of Chile in Talcahuano, Dr. Tarifeño is also carrying out a program related to physiological-ecological aspects of fish larvae.

In general, in all Chilean institutions where studies on early life history of fish are performed, the scientists are working on projects similar to those mentioned above, trying to enlarge the scope as far as possible.

A collaborative effort with FAO is presently underway. However, agreements with foreign institutions are rather rare. There are programs jointly developed by the Pontificia Universidad Católica of Chile in Talcahuano and Gothenburg University, through agreements with SAREC (Swedish Agency for Research Cooperation with Developing Countries) or direct joint projects between scientists of Instituto de Oceanología in Viña del Mar and of the Southwest Fisheries Center, La Jolla, California, on the influence of temperature on otolith growth in sardine larvae under experimental conditions. Chile has also made application to join the yet to be implemented SARP Project.

Research centers where studies on early life history of fish are carried out exist along the coasts of Chile as well as in Santiago. A list of the more active institutions and individuals presently involved include the following:

Universidad Prat, Facultad de Ciencias del Mar, Iquique:
W. Palma Saez, J.L. Pizarro, R. Correa, V. Fernandez.

Universidad del Norte, Departamento de Biología Marina, Coquimbo: A. Aron, E. Acuña, H. Flores, A. Silva.
Instituto de Oceanología, Universidad de Valparaiso, Viña del Mar: F. Balbontin, M. Garreton.
Universidad Católica de Valparaiso, Facultad de Recursos Naturales, Valparaiso: S. Palma.
Instituto de Fomento Pesquero (IFOP). Santiago: A. Asencio, A. Mujica, O. Rojas.
Universidad de Concepción, Departamento de Oceanología, Concepción: T. Antezana.
Pontificia Universidad Católica de Chile, Talcahuano. BIOTECMAR: P. Bernal, G. Herrera, Gonzalez, E. Aguilera, H. Muñoz, E. Tarifeño, A. Troncoso.
Universidad Austral de Chile, Valdivia: C. Moreno, T. Rueda, G. Valenzuela.

Ecuador

The waters of Ecuador are also under the hydrographic regime that dominates Peruvian and Chilean waters. Its coasts are not very irregular except for Guayaquil Gulf where the mouth of the Guayas River basin establishes a typical estuarine environment (García 1983). From the southeast, flows a frontal system or Frente Ecuatorial of superficial circulation, with different characteristics according to the season of the year (Enfield 1976; Pak and Zeneveld 1974). This system separates tropical superficial waters from the modified subtropical superficial ones. This is apparent during winter when the flow of the cold Humboldt Current to the northwest becomes stronger. The flow of warm waters from the north, which takes place in summer, moves it away southward. Abnormal displacements of this flow cause the "El Niño" phenomenum which produces drastic changes in biological productivity (Jiménez 1982, 1983).

French and Menz (1983) suggested that the front areas of off-shore Ecuador determine the optimum conditions for reproduction, feeding, and larval fish survival. The most intensive spawning of the chief commercial pelagic species—the mackerel *Scomber japonicus*, the sardine *Sardinops sagax*, the round sardine *Etrumeus teres*, *Opisthonema* spp., and the anchovy *Cetengraulis mysticetus*—takes place at times when oceanographic conditions are best for larval fish survival. Such conditions principally occur in the Gulf of Guayaquil.

Research on the early life history of fish in Ecuador is not very developed and deals mainly with distribution and abundance of eggs and larvae (Cajas and Hinostroza 1981 on clupeids and engraulids; Peribonio et al. 1981, Jiménez 1982, and García 1983 on the mackerel, sardine, round sardine, and other clupeids in the coastal waters of Ecuador and the Gulf of Guayaquil; García 1983 on mackerel; García et al. 1983 on sardine near the Galapagos Islands; and Garcia and Ochoa 1983 on the effect of "El Niño" on zooplankton and ichthyoplankton in Ecuadorian waters between 1983 and 1985).

The few scientists who are carrying out studies in this field are M.L. García (retired at present), L. Mariduena, D. Hinostroza, L. Cajas, Y. Ochoa, and M. Luzuriaga de Cruz, mainly in Guayaquil at the Instituto Nacional de Pesca.

As far as international collaboration is concerned, it should be mentioned that many years ago there was a development Project of FAO and that Ecuador, Chile, and Peru tried to join the yet to be implemented SARP Program.

Colombia

In Colombia, whose coasts lie mainly on the Pacific, studies on early stages of fish development have not been numerous. Greater effort has been directed to mollusks and crustaceans that have more economic importance. FAO also gave its support to such research many years ago.

In the 1970's, there were descriptive papers like those of Mercado-Silgado (1971) and Mercado-Silgado and Ciardelli (1972) on *Megalops atlanticus*, Artunduaga (1972) on *Scomberomorus sierra*, and Maldonado and Remolina (1975) on the anchovy, *C. mysticetus*. Mora-Lara (1983) in his paper on pelagic resources of Colombian waters commented on certain reproductive characteristics of some pelagic species.

Alvarez-León and Lesser (1986) in their paper on the recruitment of demersal resources, basically mollusks and crustaceans, also considered some fish species such as *Mugil* spp. and *Eugerres plumieri*. Their emphasis was the exploitation of this resource in coastal lagoons and estuaries.

The few scientists working on early life history of fishes are concentrated at the fisheries institute INDERENA in Bogota, or at Universidad Jorge Tadeo Lozano Bogota, Facultad de Ciencias del Mar, where several students have presented theses on ichthyoplankton.

Caribbean Coast

Venezuela

The coast of Venezuela lies on the Caribbean Sea. In that country very few scientists are working on ichthyoplankton and recruitment of marine fish. In the 1960's and 1970's, with the collaboration of FAO, some studies were conducted by Barrett and Howard (1961) on the anchovy, *Cetengraulis mysticetus*, Simpson (1965) on *C. edentulus*, and Simpson and Gonzalez (1967) and Lopez Rojas (1972) on the sardine, *Sardinella anchovia*. Recently, there has been increased interest in assessment of larval fish potential within the areas influenced by the predominant hydrological regime and its seasonal characteristics which have a noticeable influence on the fisheries in the country.

At the Fundación La Salle de Ciencias Naturales, Estación de Ciencias Marinas, Margarita, studies are carried out on some species such as clupeids and engraulids (Rodríguez et al. 1983, a and b) and mugilids and carangids (Rodríguez et al. (1983b). There also exists a collaboration at the personal level between the Centro Interdisciplinario de Ciencias Marinas (CICIMAR) in Baja California, Mexico, particularly in regard to clupeids and engraulids.

At INTECMAR at the Universidad Simon Bolivar in Caracas, studies on aspects of juvenile recruitment into fishing areas in demersal communities are being conducted (Penchaszadeh et al. 1986). In these investigations, ten fish species caught at the Triste Gulf are being studied. Among these ten species the most important are *Lutjanus synagris*, *Sphyraena guachancho*, *Selene setapinnis*, and *Diapterus rhombeus*.

The active Venezuelan early life-history institutions, including names of some scientists are the following:

Estación de Investigaciones Marinas (EDIMAR), Fundación La Salle, Margarita: C. Rodríguez.
Instituto Oceanográfico, Universidad de Oriente, Cumaná.
Centro de Investigaciones Científicas, Universidad de Oriente.
Instituto de Zoología Tropical, Universidad Central of Venezuela, Caracas.
Instituto de Tecnología del Mar (INTECMAR), Universidad Simon Bolivar, Caracas: P. Penchaszadeh.
Centro de Investigaciones Biológicas, Universidad de Julia, Maracaibo.

Atlantic Coast

The waters at the south-western end of South America are subject to a complicated oceanographic regime that changes seasonally and depends mainly on displacements of principal marine currents: the Brazil Current of subtropical waters flowing to the South and the Malvinas Current of subantarctic waters flowing to the North. There are also local currents and the action of large rivers such as the River La Plata, the influence of which may be noted along the shores of Argentina and Uruguay. The north-western sector of the ocean between 10° S and 10° N is under the influence of the regime of warm tropical waters and the Amazon River.

The fronts of the various water masses are of great importance to the distribution and life processes of many marine organisms. This area of the Atlantic is characterized by a large continental shelf, particularly accentuated off Argentina, that is of great importance in the development and fate of early life stages of fish.

Argentina

Studies on the early life history of fish began with the work of Ciechomski in the 1960's when the Instituto de Biologia Marina in Mar del Plata was created. This institute was later restructured and transformed into the present Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP).

At the beginning, studies were concerned with taxonomy and morphology of eggs and larvae for the purpose of identification. The research emphasis began to change with a 1967–73 FAO/Argentina Government agreement. From 1978 to 1979, agreements between Argentina, West Germany, and Japan resulted in 18 monthly cruises within Argentinan shelf waters, aboard the research vessels *Walther Herwig* and *Shinkai Maru*. Since 1981, two INIDEP-owned vessels have permitted greater continuity of data collection. It has been possible to study selectivity of plankton nets, handling of ichthyoplankton data, and sampling error (Ciechomski et al. 1983; Sánchez and Ciechomski 1984; Ciechomski and Sánchez 1986; Sánchez 1986; Ciechomski and Sánchez 1988; all in relation to anchovy (*Engraulis anchoita*) eggs and larvae.

Morphological and systematic studies of marine fish eggs and larvae have been published by Ciechomski and her collaborators since the beginning of the 1960's. Among the papers published in the 1980's are Ciechomski (1981) in summarizing the existing data in Atlas format; Ciechomski and Booman (1981) on *Macrouronus whitsoni*, *Coelorhynchus fasciatus*, *Micromesistius australis*, and *Salilota australis*; Ciechomski and Cassia (1982) on *Cynoscion striatus*; Ehrlich (1982) on *Congiopodus peruvianus*; Cassia (1984) on *Stromateus brasilianus*; Doseff and Rakitin (1987) on larvae of *Trachurus lathami*; Sánchez and Acha (1988) on scorpaenids, *Sebastes oculatus*, *Helicolenus dactylopterus lahille*, and *Pontinus rathbuni*; De Cabo (1989) on larvae of *Genypterus blacodes*, *Trypterygion cunninghami*, and *Pinguipes* spp.; Camina and Ciechomski (in press) on larvae of *Basilichthys bonaeriensis argentinensis*; and Cassia and Lasta (in press) on larvae of *Sprattus fuegensis*. Cassia is at present developing studies that allow for an early differentiation of the larvae of Engraulidae and Clupeidae living off the shore of Buenos Aires Province.

The following papers, published in the 1980's, deal with fish egg and larvae distribution in relation to environmental conditions and reproductive activity: Ciechomski et al. (1981); Ciechomski (1982) where only the Patagonian shelf is taken into consideration; Ciechomski and Booman (1983) on anchovy; Cassia and Booman (1985) on ichthyoplankton in general; Ciechomski et al. (1986a) on anchovy, including vertical distribution, and where it is shown that the majority of its eggs are distributed within the layers between 50 m and the surface; Ehrlich and Ciechomski (1986) on hake, *Merluccius hubbsi*, and its winter spawning; Ciechomski and Sánchez (1986) with a review of 20 years

of research; Lasta and Ciechomski (1988) on egg and larval distribution in Samborombon Bay, considered spawning and nursery ground for several species, and Ciechomski and Sánchez (in press) on anchovy. Also, two other papers by Hubold (1982, a and b) and Hubold and Ehrlich (1981), although published in Brazil, include work conducted in northern Argentina waters and deal with anchovy and *Brevoortia* spp., *Lycengraulis grossidens* and *Anchoa martinii* egg and larval distribution, respectively.

At present, comprehensive studies are being carried out by C. Lasta at Samborombon Bay in order to characterize this area as a spawning and nursery ground for *Brevoortia aurea*, *Mugil liza*, several species of the family Sciaenidae, and others. Other investigations on spawning and nursery grounds at Bahia Blanca relate to *Basilichthys bonariensis*, *Ramnogaster arcuata*, *Brevoortia aurea*, *Parona signata* and some species of Sciaenidae. Acha (in press) is studying early developmental stages of *Mugil liza* and other species at Mar Chiquita lagoon and Samborombon Bay. At the Instituto del Biología Marina y Pesquera "Almirante Storni" in San Antonio Oeste, L. Curtolo began studies on ichthyoplankton in San Matias Gulf (North Patagonia). At the Instituto Antartico Argentino, studies were conducted on the larval distribution of Antarctic fish species (Tomo 1981; Alder and Tomo 1987).

Studies have been performed by Ciechomski and Sánchez (1983) on the relationship between the spawning of some fish species and zooplankton abundance. Assessments of biomass of spawning adults from egg surveys and fecundity have been conducted on the hake *Merluccius hubbsi* (Ciechomski et al. 1983); the blue whiting *Micromesistius australis* (Sánchez et al. 1986); and the anchovy *Engraulis anchoita* (Ciechomski and Capezzani 1973; Ciechomski et al. 1983; Sánchez and Ciechomski 1984; Ciechomski et al. 1986a; Ciechomski and Sánchez 1988; in press).

In the paper by Ciechomski and Sánchez (1984) formulae were given to estimate daily egg production by relating age of embryos, temperature, and development stages, and by introducing a correction factor for embryonic mortality from the time of spawning up to collection. Studies have been conducted on the growth in weight and condition factor of anchovy larvae from different areas, months, and years (Ciechomski et al. 1986a; Sánchez et al., in press). All these studies, together with data on the incidence of food particles in the digestive tract, have allowed the characterization of different spawning areas in the sea, where different values in the nutritional condition factor have been detected and where differences in the larval mortality coefficients have been observed.

Two spawning areas for anchovy are considered of most interest, one near the mouth of the La Plata River and the other in the Patagonian region of the Valdez Peninsula, where a frontal system exists between stratified shelf waters and tide- and wind-homogenized coastal waters (Carreto et al. 1981; Glorioso 1987). This area is under the influence of the above mentioned frontal system and is very important for the spawning of several fish species, including hake. For this reason, it is intensively studied by specialists in the different marine sciences of INIDEP.

In studies of larval mortality, aspects such as feeding, nutritional condition factor, and advection have been considered (Ciechomski and Sánchez, in press). Also, investigations have been initiated on predatory activity on fish eggs and larvae by gelatinous plankters (H. Mianzan of the Laboratory of Zooplankton of INIDEP). Studies on cannibalism in anchovy eggs are being conducted which formerly were carried out by V. Angelescu and A. Anganuzzi of INIDEP. More details on some of these aspects can be found in Sánchez (in press).

To determine the relationship between anchovy mortality and various oceanographic and biological processes which in turn affect the variability of anchovy recruitment, a team of international scientists from Argentina, Uruguay, Brazil, Germany, Sweden, and America carried out a cruise (sponsored by the IOC of UNESCO) on board the West German RV *Meteor* in the austral spring of 1989. Details about the objectives, plans, and participants have been sent by Sánchez to the ELHS Newsletter of the A.F.S. (1989).

In INIDEP there are ichthyoplankton samples from beyond the continental slope off Argentina obtained through an agreement with the U.S.S.R. that have yet to be analyzed.

Papers on reproduction and fecundity of marine fish have been published by Christiansen and Cousseau (1985) on the anchovy, Cassia (1986) on *Cynoscion striatus*, and Christiansen et al. (1986) and Olivieri and Christiansen (1987) on the hake. Research on this subject continues, particularly to estimate anchovy, hake, and mackerel spawning stocks.

The institution where the majority of studies related to early life stages of marine fish have been conducted is the Instituto Nacional de Investigacíon y Desarrollo Pesquero, Mar del Plata. The scientists at the Laboratory of Fish Biology and Ichthyoplankton are J.D. Ciechomski, R.P. Sánchez, M.D. Ehrlich, C.A. Lasta, M.C. Cassia, and M.E. Acha. Other institutions where early life-history studies are conducted are the following:

Instituto de Biología Marina y Pesquera "Almirante Storni" in San Antonio Oeste, Prov. Río Negro: L. Curtolo.

Instituto Antártico Argentino in Buenos Aires (larvae of Antarctic fish): A. Tomo (absent at present) and V.A. Alder.

Uruguay

In this country on the Atlantic coast, where fishing activity is quite intensive, there are few studies on early life

stages of fish. Most information comes from bordering countries, mainly Argentina, where the Uruguayan waters have often been covered by cruises. The River Plata Treaty between these two countries created a common fishery zone and a common research area. This zone is markedly influenced by the La Plata River.

Uruguayans conducted some ichthyoplankton investigations from 1979 to 1983 whenever it was possible to obtain adequate materials. This research was carried out by G. Mantero at the Instituto Nacional de Pesca (INAPE) in Montevideo. She worked on the morphology of larvae and juveniles of *Peprilus paru* (Mantero 1981a), on the sciaenid *Macrodon ancylodon* (Mantero 1981b), and on the anchovy *E. anchoita* (Mantero 1983, 1986). For the latter, she described winter spawning from 1979 to 1982. She also studied the distribution of eggs and larvae of hake *Merluccius hubbsi*, *Trichirus lepturus*, and *Stromateus* sp. and assessed the spawning adult anchovy in this area from 1980 to 1981. During the last Symposium on Fisheries Investigations, held in December 1988 in Río Grande, Brazil, Nion and Ríos (1988) presented research conducted on the assessment of anchovy eggs and larvae in Uruguayan waters, together with studies on nursery grounds, mainly for the 0 group.

Other studies have included the work of Ubal et al. (1987) on the season, area, size, and structure of the spawning stock of hake, and of Grunwaldt (1986) on the fecundity of this species. Studies on early life-history stages of fish are carried out in GNAPE, Montevideo. There appears to be some interest in early life-history investigations at the Universidad de la Republica, Montevideo.

Brazil

The first publications on early life stages of fish appeared in Brazil in the 1970's. During the period 1970–1980, many papers were published by Matsuura and his collaborators, Phonlor, Weiss and her collaborators, and others. Since 1980, this research has intensified, the number of investigators increased, and new aspects have been considered. Studies have mainly been conducted off the southeastern and mid-section coasts which support large commercial fish populations. There is little information available from the northern and northeastern zones. Brazil has a very large coastline, approximately 8000 km, from 5° N up to 34° S, most of which encompasses the tropical and subtropical regions with their typical ichthyofauna.

Several species are being investigated in these studies, particularly those of economic value. One of the most important species for the Brazilian fishery is the sardine, *Sardinella brasiliensis*. In the southeastern area, the catch in 1973 reached 288000 metric tons (Matsuura 1987). The most intensive spawning and the highest density of larvae occurs between 22° and 26° C, and between 34.5 and 36‰ (Matsuura 1979). Since 1973, catches have fluctuated from year to year and now are low, while the abundance of anchovy is high (Rossi-Wongtschowski from the Instituto Oceanografico, São Paulo, pers. commun. Dec. 1988). Consequently, sardine are being intensively studied under an Integrated Research Sardine Program, in which investigations on its early stages of development are included, and in which several institutions have participated, mainly the Instituto Oceanografico in São Paulo.

Research on this species is closely related to recruitment and the estimation of spawning stocks through the egg production method. Recent papers published on the sardine include Matsuura (1986, a and b) on its exploitation, recruitment, and assessment of spawning stocks; Rossi-Wongtschowski et al. (1988) on spawning, reproductive cycle, and fecundity; and Campaner and Hondo (1987) on the co-occurrence of the copepod, *Calanoides carinatus*, and sardine larvae. Additional studies such as the estimation of the spawning stocks by Matsuura, Katsuragawa, and collaborators; larval mortality, calculated by Matsuura as 28% daily; and other studies have been carried out on the species. Also, investigations in the formation of daily increments in otoliths are being conducted.

Anchovy is another commercially important pelagic species and is shared by Brazil, Uruguay, and Argentina. Among more recent publications are Matsuura and Nakatami (1980) on methodological characteristics related to the collection of samples; Hubold (1982b) on reproductive ecology; Nakatami (1982), Weiss and Almeida (1983), and Phonlor (1984) on morphology and distribution of eggs and larvae; and Weiss et al. (in press) on egg mortality in different regions. Methodological aspects are being considered at present by Katsuragawa and others.

Publications on scombrids include larval abundance of five species of tunas between 23° and 29° S by Matsuura and Sato (1981), spawning of *Katsuwonus pelamis* by Matsuura (1982, a and b; Matsuura 1986a), and distribution of larvae of several tuna and mackerel species by Mafalda and Weiss (1988). Yoneda, Katsuragawa, and co-workers at the Instituto Oceanografico in São Paulo are developing experiments on rearing scombrid and sciaenid larvae in the laboratory.

Papers on other species include Matsuura and Katsuragawa (1981, 1985) on larvae of *Balistes capricus*; Matsuura and Yoneda (1986, 1987) on larvae of *Lophius gastrophysus*; Weiss et al. (1987) on larvae of *Antigonia capris* and *Zenopsis conchifer*; Sato and Matsuura (1986) on larvae of *Thyrsitops lepidopoides*; Weiss and Hubold (1988) on eggs and larvae of *Maurolicus muelleri*. Sadowski and Almeida-Dias (1986) and Vieira (1988) have studied *Mugil liza* and *M. platanus* and discovered a long spawning period and egg and larvae transport of the former in the inverse direction of the migration of spawning adults. Sinque et al. (1983) worked on larval distribution of Sciaenidae in Paranagua Bay.

More general studies that deal with egg and larval distribution in relation to environmental conditions are Weiss (1981); Muelbert and Weiss (1991) on ichthyoplankton in the Los Patos Lagoon; Weiss and Souto (1988) on ichthyoplankton along the southern coast of Brazil; Sinque (in press) on ichthyoplankton in Paranagua Bay; and Monteiro-Ribas and Mureb (1988) on ichthyoplankton in the zone of upwelling off Cabo Frio. There are also publications on the distribution of Antarctic fish larvae in Bransfield Straits (Sinque et al. 1986, a and b). Recently Souto (1988, a and b) has investigated reproduction and extra vitelline nutrition of sharks, *Mustelus schmitti* and *M. canis*, and Ponz-Louro and Rossi-Wongtschowski (1988) the reproduction of various species of rays.

At the Universidad de Río Grande do Sul (FURG), Departamento de Oceanografía, Weiss and her group have been working with ichthyoplankton on the shelf off Río Grande and Los Patos Lagoon. At the same university, in the Laboratorio de Bioensayos, Phonlor with his coworkers have been conducting physiological experiments on fish larvae, such as time of yolk absorption, critical period, starvation, mortality and growth at various temperatures.

Sinque and his group at the Universidad Federal do Parana have continued their studies on coastal ichthyoplankton distribution, (including the estuarine area off Parana) and on the eggs and larvae of Antarctic fish in connection with the Biomass International Program.

At the Instituto de Oceanografico, São Paulo, where intensive research on sardine is performed, Matsuura, Katsuragawa, and collaborators are also working on microdistribution in spatial and temporal series of eggs and larvae of pelagic fish in the northern littoral area of São Paulo, on comparative ontogeny of genera of the family Carangidae in the southeastern region of Brazil, and on the development and distribution of some species of the genus *Symphurus* in the same region.

At the Universidad Federal in Río de Janeiro, A.C. Teixeira and collaborators are working on mesopelagic larvae from Guanabara Bay. They also plan to study the ichthyoplankton of Antarctic fish under an agreement between Brazil and the Federal Republic of Germany.

The principal Brazilian institutions where studies on early life stages of marine fish are carried out are

Fundaçao Universidade de Río Grande do Sul (FURG), Departamento de Oceanografía, Río Grande: G. Weiss, F.M. Souto. FURG, Laboratorio de Bioensayos: G. Phonlor.

Universidad Federal de Parana, Centro de Biologia Marina, Paranagua, Parana: Ch. Sinque, S. Koblitz, and L.M. Costa.

Instituto Oceanografíco, São Paulo: Y. Matsuura, M. Katsuragawa, N.T. Yoneda, H.L. Spach, F.W. Kurtz, E.M. Kitahara, E. Futema, E. Masami.

Universidad Federal de Río de Janeiro, Instituto de Biologia, Lab. Ictioplankton: A.C. Teixeira Bonecher, A. de Souza Días Neto.

Conclusions

This review of studies of early life-history stages and recruitment in marine fish in South American countries shows that they began at the end of the 1950's with descriptive studies of eggs and larvae and progressed to studies of distribution in relation to the environment, to more highly developed studies in some countries today. Scientists and managers have agreed that an understanding of the factors that control recruitment is one of the most important requirements in fishery research today. Thus, studies on feeding, predation, and advection of eggs and larvae are considered in the context of the whole plankton community in which they occur.

Several international institutions recommend the study of early life-history stages of fish in relation to all environmental parameters, for predicting the success or failure of a year class. At present in South America, as in the other parts of the world, research on recruitment is being developed from various disciplines, including physics, meteorology, and solar energy, as the only way to explain and understand the causes that define the success of a year class. Spatio-temporal studies at the micro scale are also considered important, in order to obtain data on various aspects of population dynamics of fish embryos and larvae of different species. Finally, international cooperation has proved most valuable for encouragement and development of this discipline.

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Reproduction of Red Drum, *Sciaenops ocellatus*, in the Northcentral Gulf of Mexico: Seasonality and Spawner Biomass

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ABSTRACT

Identification of red drum *Sciaenops ocellatus* eggs, especially those in late stages of development, was found to be feasible using modal analysis of egg diameter frequency distributions. However, because of the scarcity of red drum eggs in collections, both the description of the seasonal spawning curve in 1984 and 1985 and a spawner biomass estimate in 1986 were based on larval abundance data and not egg data. Most spawning in east Louisiana (LA), Mississippi (MS), and Alabama (AL) coastal and shelf waters occurred from early September through early October when water temperatures over the shelf were decreasing rapidly from 27–29° C in early September to 24–25° C in early October. Red drum larvae used to estimate spawner biomass were collected during September 1986 over most of the east LA-MS-AL shelf with the exception of the midshelf region. The resulting first-order approximation of spawning stock in the study area, 567 metric tons (1.25 million pounds), is almost certainly an underestimate. Variability among catches of larvae from which egg production was estimated probably caused this underestimation. Sampling effort during a subsequent survey was tripled in an attempt to reduce sampling error and thus improve the accuracy of this estimate.

Introduction

Concern that overfishing of adult red drum *Sciaenops ocellatus* in offshore federal waters was seriously reducing population levels in the northern Gulf of Mexico has resulted in emergency regulations during recent years. The main impetus for the emergency management decisions which closed down the commercial fishery and limited the sport fishery for this species was the lack of precise knowledge of the biomass of adult red drum in offshore waters. Insufficient data are available to directly estimate population size; because there is no longer a directed commercial fishery for this species, stock size estimates based on commercial catches are not available. Recently, two estimates of stock size have been produced using fishery-independent data from a mark and recapture effort in northcentral Gulf waters and a Gulf-wide aerial survey (Lohoefener et al. 1988; Nichols 1988).

Because no single method for stock size assessment is without potential biases and shortcomings (Ricker 1975; Smith and Richardson 1977), another fishery-independent method, based on the production of eggs and larvae, was used in an attempt to provide additional abundance information on that portion of the red drum stock in east Louisiana, Mississippi, and Alabama waters. This paper presents the resulting first-order estimate of red drum spawner biomass based on larval abundance, new data on batch fecundity and spawning frequency, and a description of the seasonal spawning pattern in the north-central Gulf of Mexico.

Methods

Collections

Ichthyoplankton collections were taken during 11 sampling

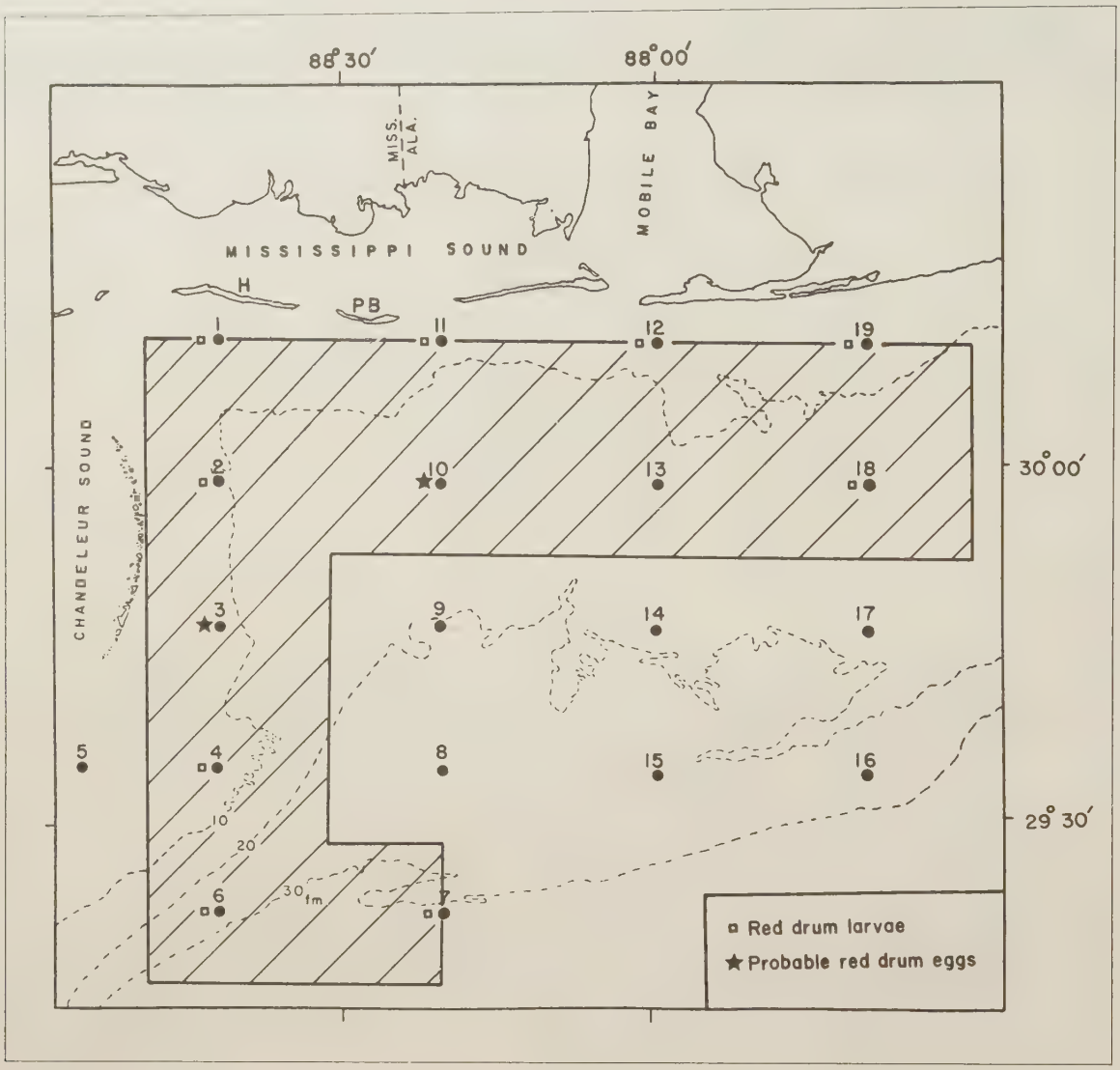

Figure 1

Occurrence of red drum eggs and larvae at nineteen locations on the east LA-MS-AL shelf during the 1986 ichthyoplanktin survey, 8–11 September. The hatched area encompasses assumed red drum spawning area. H = Horn Island; PB = Petit Bois Island.

periods (6 in 1984 and 5 in 1985) each extending 24–48 h in duration at approximate biweekly intervals from late August to early November (Lyczkowski-Shultz et al. 1988a). Additional collections were taken during a shelf-wide survey of 4 days duration, 8–11 September 1986 (Lyczkowski-Shultz 1987). Similar surveys were conducted in September 1987 and 1988. The sampling series in 1984 and 1985 were taken in Mississippi coastal waters in the near vicinity of a subsurface current drogue which identified the water mass to be sampled during a particular cruise (Lyczkowski-Shultz et al. 1988a). Collections from the 1986 survey were taken at nineteen predetermined locations on the east LA-MS-AL shelf (Fig. 1).

Collections were taken with a 1 × 1.4-m Tucker trawl with an effective mouth opening of 1 × 1 m when the net is fished at a 45° angle. The opening-closing Tucker trawl consisted of three nets with 0.333-mm mesh netting which were operated by messengers. Tow path for these collections was horizontal, and of approximately 5-minutes duration. At each station in 1986, collections were made at nominal depth strata of 1 and 5 m. A third, deeper level, usually at ⩾10 m, was sampled in 1984 and 1985.

A conductivity/temperature/depth probe (CTD) mounted 0.5 m above the Tucker trawl on the conducting/towing cable monitored sample depth and obtained vertical profiles of temperature and salinity prior to sample collection. Digital flowmeters in each Tucker trawl measured volume filtered.

Samples were preserved at sea in 5–10% buffered formalin and later (one week to six months) transferred to 70% ethanol for final preservation. In the laboratory all fish larvae were removed from either the entire sample or from a one-half aliquot using a Motoda plankton splitter. Fish eggs were removed from either the whole sample or a known aliquot, depending on the density of eggs present. A target subsample of eggs from each sample was 200. Standard length (SL) of larvae was measured to the nearest 0.1 mm at 12×; egg diameters were measured to the nearest 0.02 mm at 50× using a stereomicroscope.

Egg Identification Methodology

Egg identifications were based on descriptions of red drum egg morphology (Holt et al. 1981; Holt et al. 1988), and comparison with modal size and size-frequency characteristics of known red drum eggs collected in the study area (Lyczkowski-Shultz et al. 1988b). The identity of these eggs was established after eggs in one collection were hatched in shipboard rearing containers and the larvae reared until positive identifications were made. Comparative information on the size and morphology of eggs of co-occurring taxa was taken largely from Moser et al. (1984).

Biomass Estimation Procedure

The adult biomass of red drum was calculated with an equation modified from Houde (1977):

$$B = \frac{P_d \cdot W}{F \cdot K \cdot S},$$

where B = biomass of adults in the stock
P_d = total number of eggs spawned in one day (daily egg production)
W = mean weight of adults in the stock (when sex ratio is 1:1)
F = mean batch fecundity of females
K = proportion of adults that are females
S = proportion of females that are spawning on a particular day (spawning fraction).

The low frequency of occurrence of red drum eggs precluded estimation of spawning biomass directly from egg densities. To calculate daily egg production (P_d) from larval densities we estimated larval mortality rate and assumed that the mean density of individuals at time 0 approximated mean daily egg density. Mortality, the decline in numbers of fish over time, is the slope of the exponential function relating larval abundance and age:

$$D_t = D_0 \exp(-Zt) \quad \text{(Ricker 1975)},$$

where Dt = density of larvae at time t
D_0 = mean density of individuals at time 0 (i.e., density of eggs)
Z = instantaneous mortality coefficient
t = age of size class in days since spawning.

Size class age and densities were fitted to this exponential function with a nonlinear least squares routine using a pseudo-Gauss-Newton algorithm (Dixon and Brown 1979; Picquelle and Hewitt 1983). Ages were assigned to midpoints of the 0.5-mm size classes using the growth equation $L = 1.310 \exp(0.130\ t)$, where L = notochord or standard length and t = larval age in days. This equation described the growth of red drum larvae in September 1985 at temperatures that were similar to those found during the 1986 survey, 27.8°–29.0°C and 28.1°–29.0°C, respectively (Comyns et al. 1989). The density of each age class was corrected for stage duration by dividing the density estimate of each age class by their respective durations so that abundances of all size classes would be standardized with regard to time (Houde 1977).

Daily egg production was derived by multiplying the estimated mean egg (age 0) density by the volume of water in the spawning area. The spawning area in 1986 was defined as that portion of the survey area where red drum eggs and larvae were captured. One station (stn. 13) at which no red drum eggs or larvae were found was included in the spawning area because this station was surrounded by positive stations. The area associated with a station was taken to extend midway between that station and adjacent stations. Water volume was calculated by multiplying the area over which red drum spawned, by the depth to which collections were taken (5 m).

Data on reproductive biology of red drum came from specimens collected by purse seine from Louisiana coastal waters in the vicinity of the mouth of the Mississippi River in September of 1986, 1987, and 1988, when spawning was assumed to be at or near its peak (Wilson et al. 1988). The red drum larvae used in the present study were collected just east of the Mississippi River mouth in Mississippi coastal waters. We assumed that reproductive parameters of red drum from these adjacent localities would not differ because the results of mark and recapture, electrophoretic, and morphological studies indicate that red drum in the Gulf of Mexico form a single genetic stock (Ramsey and Wakeman 1987; Nichols 1988; Poss 1988; Wakeman and Ramsey 1988).

Batch fecundity of an individual was determined from numbers of hydrated oocytes in six subsamples of ovarian tissue (Hunter et al. 1985; Wilson et al. 1988). Spawning females, i.e. fish that had spawned within 24 hours of sampling, were identified by the presence of post-ovulatory follicles in ovarian tissue (Hunter and Macewicz 1985; Fitzhugh et al. 1988; Wilson et al. 1988). Spawning fraction was the ratio of spawning females to the total number of

Table 1

Summary of collection dates, effort, frequency of occurrence, and mean density (all sampling depths and times combined) of *Sciaenops ocellatus* larvae captured near the subsurface current drogue in waters of the northcentral Gulf of Mexico during late summer and fall months 1984–85.

Cruise	Date	Total volume filtered (m^3)	No. of collections	Occurrence		No. of specimens	Mean density (Number per 100 m^3)	
				frequency	percent		All collections	Positive collections
84-8	30–31 Aug. 1984	1117	9	3	33	15	1.34	3.97
84-9-1	13–14 Sept. 1984	7427	29	28	97	5839	78.62	82.29
84-9-2	26–27 Sept. 1984	3016	10	9	90	256	8.49	9.12
84-10-1	10–11 Oct. 1984	4480	13	12	92	606	13.53	14.35
84-10-2	23–25 Oct. 1984	5016	19	1	5	2	0.04	0.63
84-11	07–09 Nov. 1984	2739	9	0	0	0	0	0
85-8	28 Aug. 1985	897	3	1	33	4	0.45	1.20
85-9-1	11–12 Sept. 1985	6864	27	21	78	447	6.51	8.44
85-9-2	25–26 Sept. 1985	2284	8	5	63	19	0.83	1.40
85-10	10–11 Oct. 1985	2445	9	7	78	54	2.21	2.90
85-11	4 Nov. 1985	1257	5	1	20	1	0.08	0.35

mature females in the sample. The inverse of this ratio estimates the time in days between successive spawnings and approximates spawning frequency. Mean batch fecundity and spawning fraction were determined from observations made in September of 1986, 1987, and 1988. Data from three years were combined because of the relatively small sample sizes in each individual year. Estimates of mean weight and sex ratio were calculated from observations made in September 1986.

Age in days of red drum larvae used to backcalculate spawning dates during the 1984 and 1985 seasons was determined from growth equations and/or raw length-at-age data using counts of daily increments in sagittae of larvae from the same collections or from collections where water temperatures were most similar (Comyns et al. 1989). Approximate spawning dates were estimated for each cruise in 1984 and 85 by subtracting the modal age in days (or range in age when no mode was present) from the capture date.

Results

Occurrence of Red Drum Eggs

Examination of 38 collections from 11 sampling series conducted in late August to early November 1984 and 1985, and examination of 125 collections taken during shelfwide surveys in September of 1986, 1987, and 1988, resulted in only four occurrences of red drum eggs.

Physical Environment

From September to early November the water column in the sampling region was relatively well mixed (Lyczkowski-Shultz et al. 1988a). Temperatures generally ranged from 27 to 29°C in August and September, from 24 to 26°C in October, and from 22 to 23°C in early November. A seasonal trend in salinity was not as evident. Salinities within the upper 13 m generally ranged from 25 to 34 ppt in August and September, from 28 to 34 ppt in October, and from 32 to 35 ppt in early November.

Spawning Seasonality

Seasonal Patterns in Abundance—Patterns of seasonal abundance of red drum larvae were consistent in 1984 and 1985. Red drum larvae were most numerous in mid-September. Mean larval density (number of larvae per 100 m^3, all collections) in mid-September 1984 and 1985 was 78.6 and 6.5, respectively (Table 1). Lowest larval abundances were found in August and late October–November, when densities never exceeded 1.4. Observed spawning dates for red drum in LA-MS-AL coastal waters ranged from 21 August to 2 November (Table 2). Spawning dates backcalculated from collections during time of maximum larval abundance for each year were 7 and 8 September 1984 and 2, 6, and 9 September 1985.

Biomass Estimate of Spawning Stock

Spawning Area—During the 1986 survey a total of 347 red drum larvae were collected at nine of the nineteen stations and probable red drum eggs were collected at two stations (Table 3). The spawning area generally enveloped the 10-fm bottom contour and was estimated to cover 6.497×10^9 m^2 (Fig. 1). Red drum spawning does occur in

Table 2
Range in age and age of modal size class(es) (to the nearest 0.5 day) of red drum larvae collected during cruises from 1984–85. Backcalculated spawning dates were based on age of modal size class(es) except where no mode was present, then spawning date was calculated from the range in age.

Cruise	Date	Range in age (days)	Modal age (days)	Approx. spawning date
84-8	30–31 Aug. 1984	3.0 - 7.5	5.0	25 Aug.
84-9-1	13–14 Sept. 1984	2.0 - 8.0	5.0	8 Sept.
84-9-2	26–27 Sept. 1984	2.0 - 7.5	5.0	21 Sept.
84-10-1	10–11 Oct. 1984	4.0 - 20.0	7.5,9.0	3 Oct, 30 Sept.
84-10-2	23–25 Oct. 1984	—	6.5	18 Oct.
85-8	28 Aug. 1985	3.0 - 6.5	—	25, 21 Aug.
85-9-1	11–12 Sept. 1985	2.0 - 12.0	2.0,9.5	9, 2 Sept.
85-9-2	25–26 Sept. 1985	2.0 - 7.0	2.0	23 Sept.
85-10	10–11 Oct. 1985	2.0 - 11.0	6.0	4 Oct.
85-11	4 Nov. 1985	—	2.0	2 Nov.

Chandeleur Sound, but this area was not included in the 1986 survey. The volume of water used in estimating total daily egg production was approximately 3.249×10^{10} m^3.

Larval Mortality and Daily Egg Production—Mean density of red drum larvae within the spawning area (Figure 1) was 5.06 larvae per 100 m^3 (SE = 2.01). Examination of the overall size-frequency distribution of red drum larvae from the 1986 survey indicated the presence of two size groups (Fig. 2). If combined, the less abundant group of smaller larvae would reduce the estimated mortality rate, not because mortality within this cohort was necessarily lower, but because there were fewer individuals in this cohort owing probably to either sampling variability or lower spawning intensity. Consequently, mortality and mean egg density estimates were derived only from the five older 0.5-mm size classes (3–5 mm).

The exponential function describing the nonlinear regression of duration-corrected age class densities (Table 4) on age for 3–5 mm red drum larvae was (Fig. 3):

$$D_t = 43.8 \exp(-0.521\, t),$$

where 43.8 = mean density at time 0 (No. per 100 m^3), i.e. mean daily egg density, with a standard error of 68.78

0.521 = instantaneous mortality rate with a standard error of 0.207.

Daily egg production, estimated by multiplying mean daily egg density by the volume of water encompassing the 1986 spawning area, was 1.4229×10^{10} eggs per day. The standard error of this estimate was 2.23×10^{10} eggs per day.

Sex Ratio and Mean Weight—The sex ratio (K) was assumed to be 1:1. Actual values were 51% male and 49% female (n = 327). Mean weight (W) was 8.517 kg (n = 325, SE = 2.332). Although mean weight of females is greater than mean weight of males, overall mean weight can be used in the biomass formula because the sex ratio is approximately 1:1.

Mean Batch Fecundity (F) and Spawning Fraction (S)—Mean batch fecundity was 2.128×10^6 eggs (n = 15, SE = 0.164×10^6). This estimate of mean batch fecundity is probably underestimated because purse seine sampling could be conducted only during daylight hours but red drum do not begin spawning until after dark (Holt et al. 1985). Consequently, eggs that would hydrate just prior to spawning would not have been included in estimates of mean batch fecundity. Mean spawning fraction, determined from the percentage of females with post-ovulatory follicles in ovarian tissue, was 0.20 (n = 245, SE = 0.045), indicating a spawning frequency of approximately once every five days in September.

Biomass Estimate—Incorporation of estimates of P_d, W, F, K, and S into the biomass equation resulted in an estimated spawner biomass of 567 metric tons (1.25×10^6 lb).

Discussion

Unlike most sciaenids in northcentral Gulf waters, the red drum has a restricted spawning period. Based on larval age and abundance data, red drum spawning in 1984 and 1985 extended from August until late October or early November, with peak spawning in September. During the

Table 3

Catch summary for red drum eggs and larvae collected during an ichthyoplankton survey of east LA-MS-AL shelf and coastal waters, 8–11 September 1986.

Station	Date	Time	Volume filtered (m^3)	Sampling depth	Eggs		Larvae	
					Total no.	No. per 100 m^3	Total no.	No. per 100 m^3
01	09/08/86	1807	504.5	5	0	0.00	0	0.00
01	09/08/86	1812	313.9	1	0	0.00	4	1.27
02	09/08/86	0000	284.8	1	0	0.00	4	1.40
02	09/08/86	0005	303.4	5	0	0.00	4	1.32
03	09/09/86	0325	267.8	1	2240	836.00	0	0.00
03	09/09/86	0329	266.1	5	0	0.00	0	0.00
04	09/09/86	0729	255.0	5	0	0.00	24	9.41
04	09/09/86	0734	309.0	1	0	0.00	4	1.29
05[a]	09/09/86	1201	231.6	5	0	0.00	0	0.00
05[a]	09/09/86	1206	221.9	1	0	0.00	0	0.00
06	09/09/86	1616	374.7	5	0	0.00	40	10.68
06	09/09/86	1621	311.9	1	0	0.00	4	1.28
07	09/09/86	1959	262.4	1	0	0.00	1	0.38
07	09/09/86	2004	165.8	5	0	0.00	0	0.00
08[a]	09/09/86	2240	212.5	1	0	0.00	0	0.00
08[a]	09/09/86	2245	192.3	5	0	0.00	0	0.00
09[a]	09/10/86	0149	234.8	1	0	0.00	0	0.00
09[a]	09/10/86	0154	262.0	5	0	0.00	0	0.00
10	09/10/86	0444	268.8	1	24	9.00	0	0.00
10	09/10/86	0449	227.3	5	0	0.00	0	0.00
11	09/10/86	0733	376.2	5	0	0.00	4	1.06
11	09/10/86	0739	222.9	1	0	0.00	4	1.79
12	09/10/86	1124	300.8	5	0	0.00	66	21.94
12	09/10/86	1130	212.9	1	0	0.00	106	49.79
13	09/10/86	1348	242.9	5	0	0.00	0	0.00
13	09/10/86	1353	215.0	1	0	0.00	0	0.00
14[a]	09/10/86	1558	321.3	5	0	0.00	0	0.00
14[a]	09/10/86	1603	253.0	1	0	0.00	0	0.00
15[a]	09/10/86	1857	327.3	1	0	0.00	0	0.00
15[a]	09/10/86	1901	404.1	5	0	0.00	0	0.00
16[a]	09/10/86	2123	216.7	1	0	0.00	0	0.00
16[a]	09/10/86	2129	213.1	5	0	0.00	0	0.00
17[a]	09/10/86	2310	264.0	1	0	0.00	0	0.00
17[a]	09/10/86	2315	222.8	5	0	0.00	0	0.00
18	09/11/86	0130	259.5	1	0	0.00	2	0.77
18	09/11/86	0135	281.6	5	0	0.00	0	0.00
19	09/11/86	0419	360.1	1	0	0.00	12	3.33
19	09/11/86	0424	274.7	5	0	0.00	68	24.71

[a]Stations were not considered to be in spawning area and were consequently omitted from calculations of larval density and water volume.

period of peak spawning, water temperatures over the shelf decreased from 27–29°C in early September to 24–25°C in early October 1984 and 1985. Although our collections did not extend beyond early November, water temperatures in November 1984 and 1985 were already approaching 20°C, the lower limit for spawning in this species (Holt et al. 1981). Data on the reproductive biology of red drum from the northcentral Gulf of Mexico also indicated a restricted spawning season, with gonosomatic indices of both sexes and oocyte maturity peaking in September (Wilson et al. 1988). Peters and McMichael (1987) noted that within-season spawning peaks of red drum in the Tampa Bay area of Florida were associated with new and full moons. Our data agree with these observations. Peak spawning in east LA-MS-AL coastal waters occurred within a week of the September full moon in 1984 and 1985.

In order to estimate egg production from egg or larva data, samples should be representative of the entire seasonal and areal extent of spawning. Temporal coverage of spawning in species with relatively short spawning seasons, like red drum, may not be as critical if the time

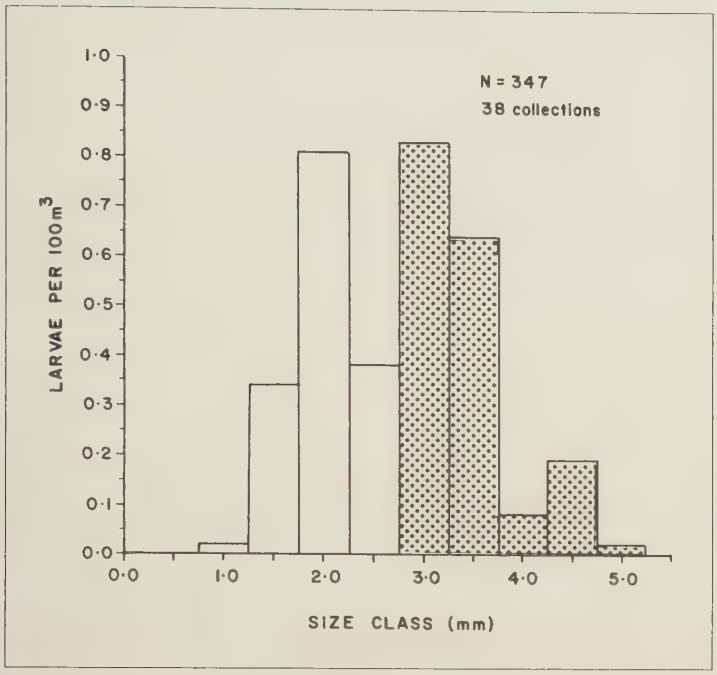

Figure 2
Size frequency distribution of red drum larvae captured during the 1986 survey of east LA-MS-AL shelf and coastal waters. Shaded size classes were used to estimate larval mortality and mean egg density.

Table 4
Age and duration-corrected density of size classes used to estimate mortality rate of red drum larvae.

Size class (mm)	Mean age (days)	Stage duration (days)	Density (#/100 m^3)	Duration corrected density
3.0–3.4	6.99	1.19	1.268	1.065
3.5–3.9	8.09	1.03	0.976	0.948
4.0–4.4	9.05	0.90	0.117	0.130
4.5–4.9	9.91	0.81	0.291	0.359
5.0–5.4	10.68	0.74	0.029	0.039

of most active spawning is sampled or a representative sample of spawning is obtained (Smith and Richardson 1977; Smith and Hewitt 1985). The assumption that the September 1986 survey was conducted when red drum were most actively spawning is supported by historical data on adult gonadal condition, as well as, temporal abundance patterns of larvae and postlarvae.

The spawning area represented by our 1986 collections is only a portion of red drum spawning grounds in the Gulf of Mexico, which include inner shelf and coastal waters from Mexico to the Everglades. That our survey area represents a logical unit or stratum in which to estimate spawner biomass is supported by recent Gulfwide stock assessment data from mark/recapture and aerial survey studies (Lohoefener et al. 1988; Nichols 1988). These data indicate that the biomass of red drum along the northwest Florida coast, ie. the area east of our study area, is very low compared to the area off Alabama, Mississippi, and Louisiana. We have assumed, therefore, that spawning activity east of our study area is minimal. To the west of our study site, the Mississippi River delta restricted movement of adults into and out of our survey area during the 3 to 4 days over which spawning activity (egg and larval production) was measured in 1986. Nichol's (1988) tag recapture data support this contention in that few fish were found to have crossed the river mouth during his study.

Egg production can be calculated either directly from egg abundance or indirectly from larva abundance if larval mortality rate can be calculated (Sette and Ahlstrom 1948; Houde 1977; Parker 1980, McGowan and Richards 1986). In this study, egg production was back calculated from larval densities because of the low frequency of occurrence of red drum eggs, caused most likely by the short incubation period (1 day) (Holt et al. 1985; Holt et al. 1988) and highly contagious spatial distribution of the eggs. Use of larvae instead of eggs to calculate egg production can cause numerous problems which may bias and, most certainly, reduce precision of the resultant spawner biomass estimate. Foremost among these problems is that eggs and newly hatched larvae may experience different mortality rates, being either higher (Smith 1973; Houde 1977) or lower (Picquelle and Hewitt 1983), than older larvae. The direction and magnitude of ontogenetic differences in mortality rate of red drum is unknown.

Another serious limitation in estimating egg production from larval densities is the highly variable nature of larval catches on which the slope of the larval abundance vs. age regression, ie. instantaneous mortality rate (Z), is based. To calculate a meaningful value of Z, larval density must

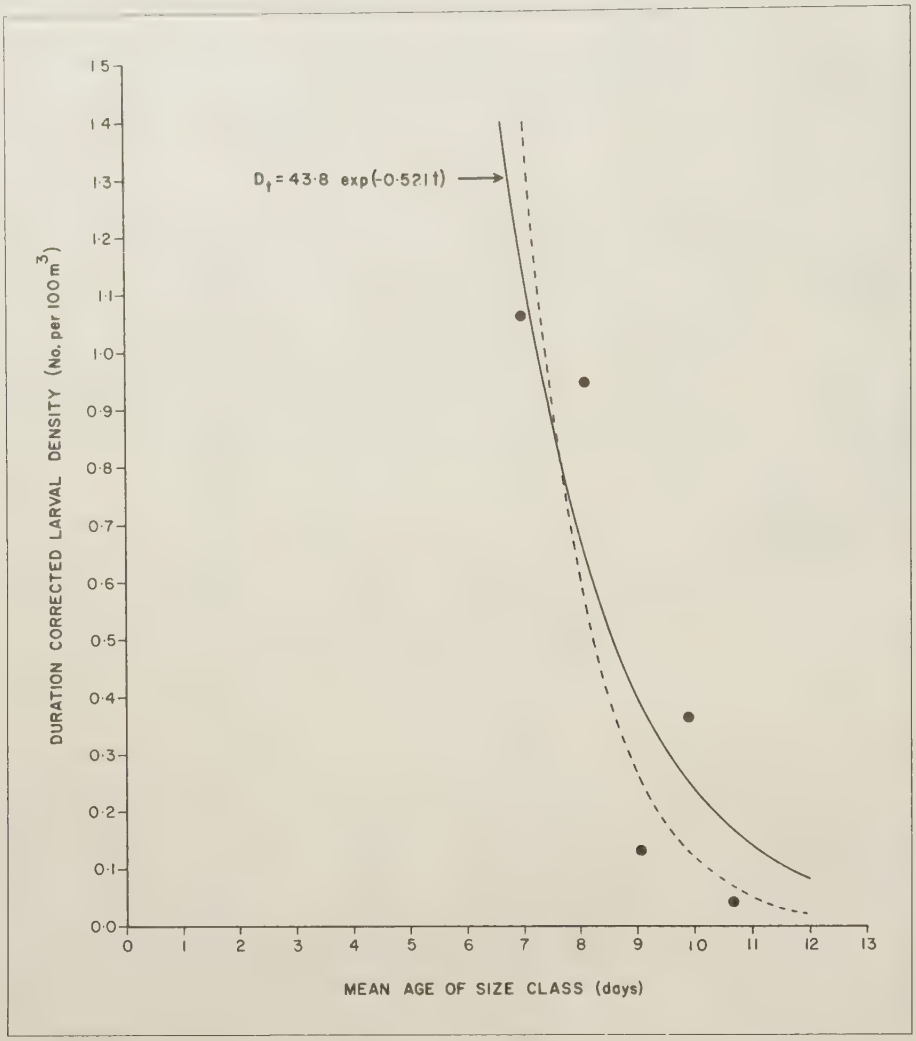

Figure 3
The relationship between duration corrected density and mean age of 3.0–5.0 mm size classes of red drum larvae. The solid line describes the exponential function of the data fitted to a nonlinear regression, and the dashed line describes the exponential function solved using log transformed density data.

be accurately measured, and an adequate range in size classes must be represented so that the descending limb of the size-frequency distribution approximates the exponential decline of larval abundance with age. In September 1986, Z was estimated to be 0.521 (SE = 0.207), which equals a daily loss of 40.6% per day ([1 – exp 0.521] × 100). This rate is similar to Z values of 0.36 and 0.64 that have been reported for another sciaenid, *Cynoscion nebulosus*, off Florida (Peebles and Tolley 1988). In an earlier calculation of the 1986 red drum spawner biomass (Lyczkowski-Shultz et al. 1988b), the same data were fitted to the exponential function using a logarithmic transformation, resulting in a steeper slope (Z = 0.81) and a spawner biomass estimate of 11.7 million pounds (Fig. 3). Examination of residuals later showed the logarithmic transformation of these data to be inappropriate.

Estimates of larval fish mortality can also be affected by two potential biases associated with sampling gear: incomplete recruitment to the sampling gear by the smallest larvae and avoidance of sampling gear by the largest larvae. Using the extensive larval red drum data sets from the 1984 and 1985 seasons, we determined that these sources of bias did not affect the mortality estimate. The shape of length-frequency distributions from over 200 collections indicated that the 3.0-mm size class, the smallest size class used in the mortality estimate, was fully recruited to the sampling gear used in this study. Comparison of daytime and nighttime collections showed no pattern of increasing catches of larvae within the larger size classes on which the 1986 mortality estimate was based (Lyczkowski-Shultz et al. 1988a), indicating that gear avoidance during daylight was not a factor.

Collections during the September 1986 survey were taken at 1 and 5 m because preliminary data from the 1984 and 1985 spawning seasons suggested that red drum larvae were concentrated in the upper 5 m of the water column (Lyczkowski-Shultz et al. 1988a). This premise is supported with data from 130 discrete-depth samples collected in the study area during five cruises in September of 1984, 1985, and 1987, when depths below 5 m were sampled; mean

density in the upper 5 m was 34.2 larvae per 100 m^3, while mean density between 7 and 12 m (the maximum depth sampled) was only 3.7 larvae per 100 m^3 (Lyczkowski-Shultz et al. 1988a; Lyczkowski-Shultz, unpubl. data). If the low density of larvae found between 7 and 12 m had extended throughout the entire water column (mean water depth was 17 m), larval abundance and the subsequent biomass estimate could have been underestimated by up to 25%.

Net movement of red drum larvae into or out of the survey area could potentially bias measurement of egg and larval production, ie. spawning activity. However, recent published reports (Chuang et al. 1982; Schroeder et al. 1985; Dinnel 1988), as well as our own observations on surface water circulation patterns over the LA-MS-AL shelf (Lyczkowski-Shultz et al. 1988a), clearly show that there is no consistent and predictable pattern of larval transport into or out of the survey area. Additional evidence showing that inshore displacement of larvae was negligible was the absence of an accumulation of larger and older red drum larvae at a nearshore sampling site located approximately 15 to 19 km NNW of the offshore sampling sites in 1984 and 1985.

Our estimate of red drum spawner biomass in north-central Gulf waters, 1.25 million pounds, is lower than estimates from two other recent stock assessments. A mark/recapture study (Nichols 1988) estimated the spawning stock between Pensacola, FL and Galveston, TX to be 90 million pounds. Seventeen percent of the stock, 15 million pounds, was estimated to occur between the Mississippi River Delta and Mobile Bay (Scott Nichols, NMFS, Southeast Fisheries Center, Pascagoula, MS, pers. commun. Jan. 1989), an area covering not only the spawning grounds delimited in this study, but also the Chandeleur Sound region where red drum spawning is known to occur. Also, aerial surveys conducted between the Mississippi River Delta and Mobile Bay in the fall of 1987 estimated the biomass of near-surface schools of red drum between the shoreline and the 12-fm contour to be approximately 11.4 million pounds (Lohoefener et al. 1988). Further indication that we underestimated the size of the spawning stock are reports from the late 1970's of individual schools of red drum in the study area that alone were estimated from aerial observations to have exceeded our biomass estimate (Overstreet 1983).

This underestimation of the spawner biomass of red drum in the study area was most likely caused by an underestimate of mean daily egg production. This estimate is not only inaccurate, it is also imprecise considering the large standard error associated with daily egg production. Although factors such as a higher mortality rate among eggs and newly hatched larvae than among older larvae (Houde 1977), or sampling only the upper 5 m, could have contributed to this underestimation of spawner biomass, the variability associated with larval catch data was most likely the primary cause. Parker (1980) found that the estimate of egg production in the northern anchovy contributed approximately 8 times more to the coefficient of variation of the spawner biomass estimate than all other parameters combined. Sampling effort within the survey area was tripled in September 1989 using oblique tows in an attempt to increase the precision of the estimate of larval red drum abundance and thus provide a more accurate and reliable estimate of red drum spawner biomass.

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Larval Distribution and Abundance of the Scombridae in Campeche Sound, with Emphasis on the Frigate Tunas (*Auxis* spp.)

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ABSTRACT

Ichthyoplankton samples were obtained using double oblique tows of a paired 61-cm bongo net containing filter meshes of 0.505 and 0.333 mm during the COSMA 16-72 cruise undertaken 8–14 August, 1972 aboard the RV *Virgilio Uribe*. Sample depths varied between 7 and 167 m. Temperature and salinity at a depth of 5 m averaged 27.7°C and 36.9 ppt, respectively, at the sampling stations. Eight scombrid species or species complexes were represented in the following percentages per 10 m^2 of sea surface: frigate tunas (*Auxis* spp.) 77%; little tunny (*Euthynnus alletteratus*) 7%; bigeye tuna (*Thunnus obesus*) 2%; blackfin tuna (*T. atlanticus*) 1%; king mackerel (*Scomberomorus cavalla*) 1%; Spanish mackerel (*S. maculatus*) 1%; yellowfin tuna (*T. albacares*) <1%; and skipjack tuna (*Katsuwonus pelamis*) <1%. *Thunnus* spp. identifiable only to genus comprised 11% of the larvae. The frigate tunas were the most abundant group, with a total of 4473 larvae per 10 m^2 of sea surface. Based on larval abundance of the smallest size class represented, the reproductive biomass of the frigate tuna complex was estimated to be 163868 metric tons. The daily mortality coefficient for the frigate tuna larvae was estimated to be 0.346. The results showed that the frigate tunas are a potential fishery resource in the area.

Introduction

Much interest has been shown in ichthyoplankton research for the detection and evaluation of potentially important fishery resources. Studies of eggs and larvae provide a means of establishing breeding times and areas of the adults. They also provide, within reliable limits, estimates of adult biomass and natural mortality during the early life phases.

The tunas are targets of one of the most economically important fisheries in the world. Large schools of bluefin, yellowfin, blackfin, and skipjack tunas have been reported in the Gulf of Mexico (Bullis 1955; Carranza 1956; Montolio and Juárez 1976; Richards et al. 1981). However, from 1964 to 1975 tuna harvests in the Mexican Exclusive Economic Zone of the Gulf of Mexico totaled only 50% of the average annual catch by the Mexican tuna fleet in the Pacific Ocean (Secretaría de Pesca 1987).

This study provides information on the distribution and abundance of the scombrid species in Campeche Sound, and establishes, based on an estimate of the reproductive biomass, that the frigate tunas are a resource with potential for commercial exploitation in the region.

Materials and Methods

Ichthyoplankton samples were obtained during the COSMA 16-72 cruise on the RV *Virgilio Uribe* on 8–14 August, 1972. The cruise was part of the international

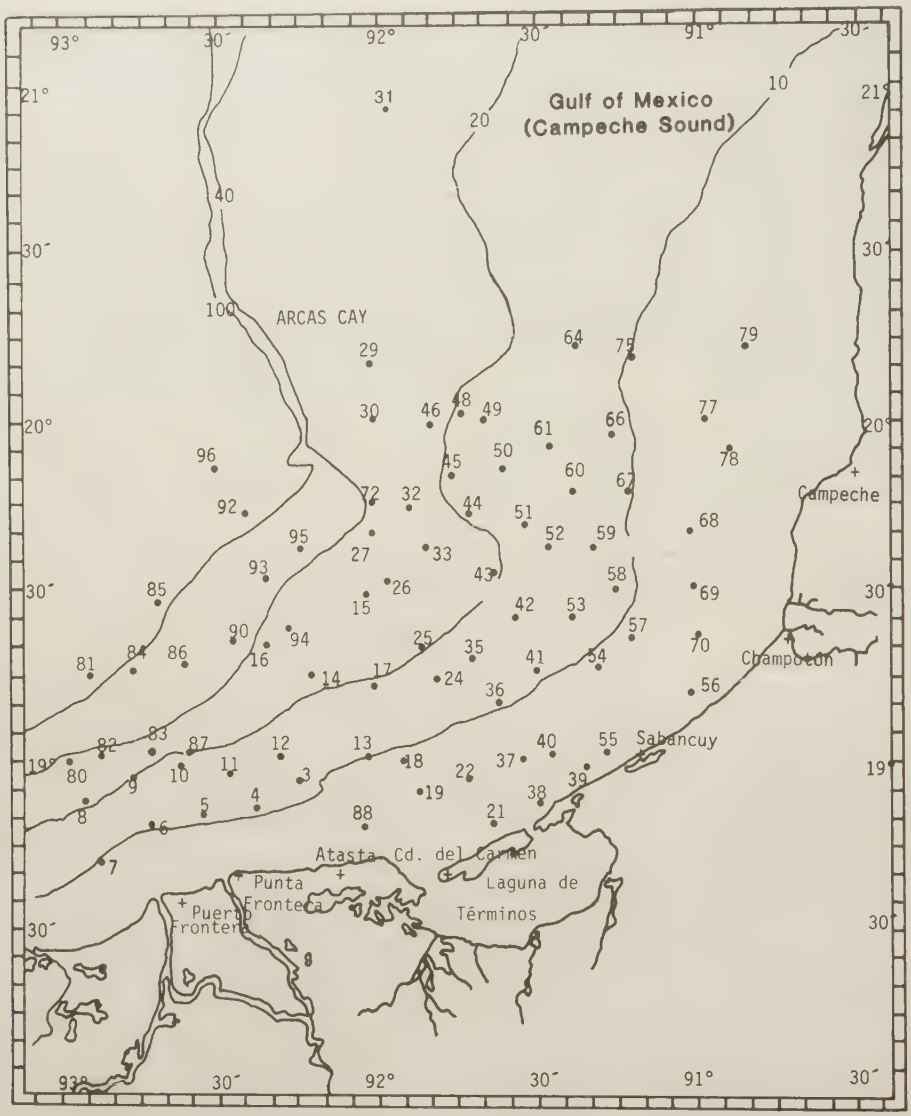

Figure 1
Map of the Campeche Sound showing the 80 sampling stations used during the COSMA 16-72 cruise. Depth contours are in fathoms.

agreement on Cooperative Research in the Caribbean and Adjacent Regions (CICAR). A total of 80 stations were located between lat. 18°40′00″–20°53′12″N and long. 90°50′06″–92°58′00″W (Fig. 1).

Samples were collected using oblique tows according to methods described by Kramer et al. (1972) and Smith and Richardson (1977). A bongo net with mouth diameter of 0.61 cm and filter meshes of 0.505 mm and 0.333 mm was towed to a maximum depth of 200 m, or to the depth dictated by the maximum depth of the station. The net was towed at an average velocity of 1.25 $m \cdot s^{-1}$ (2.5 knots), and at deployment and recovery rates of 50 $m \cdot min^{-1}$ and 20 $m \cdot min^{-1}$, respectively. Wire angles were determined for each 10 m of wire recovered throughout the tow. Calibrated flowmeters were used in the mouth of each net.

The plankton samples were fixed in a 10% formalin-seawater solution buffered with saturated sodium borate. The scombrid larvae were separated from the total sample and identified to the lowest taxon possible based on pigmentation patterns, primarily on the upper and lower parts of the caudal peduncle, the fore- and mid-brain, and the extreme upper and lower area of the snout. The height and number of spines on the first dorsal fin, and the number of myomeres and vertebrae were taken into account (Jones 1959; Matsumoto 1959, 1962; Ueyanagi 1963; Juárez 1972, 1976; Matsumoto et al. 1972; Nishikawa and Rimmer 1987). The clearing and staining technique of Hollister (1934) was used when necessary, especially for separation of bigeye tuna, *Thunnus obesus*, blackfin tuna, *T. atlanticus*, and yellowfin tuna, *T. albacares*. The frigate tunas (*Auxis thazard* and *A. rochei*) are difficult to distinguish as larvae (Uchida 1981), so identification was made only to the genus level. Standard length (SL) was measured to the nearest 0.1 mm with a stereoscopic microscope equipped with an ocular micrometer.

The absolute abundance of larvae at each station was standarized relative to 10 m^2 of sea surface according to Kramer et al.'s (1972) formula:

$$N_j = \frac{C_j Z_j}{V_j} 10, \quad (1)$$

where N_j is the number of larvae per 10 m^2 of sea surface at station j, C_j is the catch of larvae at station j, Z_j is the maximum tow depth in meters at station j, and V_j is the volume of water filtered in cubic meters at station j. Chi-square analysis was employed to test for differences in the standarized catches of each species in daytime versus nighttime hauls.

Larval Abundance

The standardized abundance estimates based on the stations positive for frigate tunas were plotted as contours over the sampling area. The area of each contour was measured with a planimeter and divided among the positive stations to obtain the area represented by each station (Sette and Ahlstrom 1948). The total number of larvae (P_j) in the area represented by station j was calculated by length class as

$$P_j = \frac{C_j Z_j}{V_j} A_j, \quad (2)$$

where A_j is the area in square meters represented by station j, and all other parameters are as in Equation 1.

The total number of larvae (P_i) by length class over the entire area represented by the positive stations was calculated as

$$P_i = \sum_{j=1}^{J} P_j, \quad (3)$$

where J is the number of stations positive for frigate tunas during the cruise (Richards et al. 1981).

An estimate of the total larval production (P_a) of frigate tuna of the smallest length class, 2.25–2.75 mm (the 2.5-mm class), during the spawning season was obtained by

$$P_a = \frac{P_i D}{d}, \quad (4)$$

where D is the number of days in the spawning season, and d is the residence time in days of the larvae in the 2.5-mm length class (Richards et al. 1981). The duration of the reproductive period was assumed to be 180 days (April–September) based on larval occurrence data in the western Atlantic, Gulf of Mexico, and adjacent regions reported by Klawe and Shimada (1959), Tibbo and Beckett (1972), Juárez (1976), and Ramírez and Ornelas (in press). Residence time, d, was calculated using a modification of a regression, $L = 2.66\ e^{0.06T}$ where L is length in millimeters and T is age in days, fitted to size at age data from the rearing studies of little tunny (*Euthynnus alletteratus*) larvae by Houde and Richards (1969). Since the smallest frigate tuna larvae collected in our study were about 2.00 mm, we assumed that the hatch length and the equation's intercept equal 2.00 and that the exponent is the same as for little tunny. The modified growth equation converted to predict age from length was

$$T = \frac{\ln L - \ln 2.0}{0.06}. \quad (5)$$

The P_a estimate was adjusted to age 0 (P_{adj}) using our estimate of the daily mortality rate (below) by substituting P_a for P in Equation 7 and solving for P_o.

Reproductive Biomass

The reproductive biomass was determined based on the relative fecundity, sex ratio, and number of larvae produced during the spawning season (Saville 1964; Ahlstrom 1968). The following equation relates these variables:

$$B_a = \frac{P_{adj}}{F_r K}, \quad (6)$$

where B_a is the biomass of reproductive adults in grams, P_{adj} is the P_a estimate adjusted to age 0, F_r is the average relative fecundity (eggs produced per gram of adult female), and K is the proportion of adults that are females. The average relative fecundity was estimated based on Simmons and McDade's (1973) equation for female *Auxis* sp. of 36.0 to 45.5 cm fork length, $F = -127.262 + 0.542\ FL$, where F is the number of eggs ($\times 1000$) in the most advanced mode, and FL is the fork length in millimeters. Body weights of adult frigate tunas were obtained using the length-weight relationship of Ishida (1971) for *Auxis rochei* captured in Japanese waters, $W = 6.05 \times 10^{-3}\ FL^{3.3}$, where W is the body weight in grams and FL is the fork length in centimeters. There are no similar data for frigate tuna in the Atlantic. Thus, female frigate tuna averaging 40.2 cm FL (W = 1190 g) in the Campeche Sound were assumed to have a relative fecundity of 76 eggs·g^{-1}. Sex ratios have not been determined for the frigate tunas in the western Atlantic. Therefore, a 1:1 male to female relationship (K = 0.5) was assumed based on studies in other areas, although significant deviations from this value have been reported (Uchida 1981).

Larval Mortality Rate

The daily mortality rate (M) for frigate tuna larvae was calculated using an exponential function

$$P = P_0 e^{-MT} \quad (7)$$

fitted to the number of larvae caught (P) by length class summed over the positive stations versus the age (T) corresponding to the midpoint of each length class estimated using Equation 5. P_0 is the absolute abundance at age 0.

Results

Larval Distribution and Abundance

The 80 stations sampled during the COSMA 16-72 cruise were located on the continental shelf (Fig. 1). Station locations, depths of tows, water volumes filtered, and environmental data are presented in Table 1. Capture data for the Scombridae are presented in Table 2. The capture percentages indicate that the most abundant categories were the frigate tunas, *Thunnus* spp. not identifiable to

Table 1

Station locations, sampling data, and environmental data for the COSMA 16-72 cruise. Only stations positive for Scombridae are included.

Station	Position		Date	Hour	Volume of water strained (m^3)	Depth of tow (m)	Physical and chemical date		
	Lat. N.	Long. W.					Depth (m)	Temp. (°C)	Salinity (ppt)
3	18°55′58″	92°13′24″	09/08/72	14:00	152.7	20.0	5.0	28.08	37.12
							10.0	27.72	37.09
4	18°51′36″	92°22′30″	09/08/72	11:15	190.4	18.0	5.0	27.84	36.99
							10.0	27.62	36.01
8	18°52′48″	92°54′48″	08/08/72	13:55	207.5	44.0	5.0	29.20	34.70
							10.0	27.52	37.06
							20.0	24.77	36.82
							40.0	23.40	36.84
9	18°57′00″	92°45′48″	08/08/72	20:23	170.7	50.4	5.0	27.62	36.67
							10.0	27.50	37.03
							20.0	27.60	37.10
							40.0	27.78	36.86
10	18°58′12″	92°36′00″	09/08/72	00:40	136.3	25.2	5.0	27.72	37.05
							10.0	27.61	37.07
							20.0	27.60	37.05
12	19°05′00″	92°17′00″	09/08/72	15:20	149.9	19.8	5.0	28.03	37.05
							10.0	28.81	37.05
13	19°05′00″	92°08′00″	10/08/72	15:18	122.0	22.0	5.0	27.92	36.00
							10.0	27.92	36.92
14	19°15′18″	92°12′12″	10/08/72	03:59	133.3	21.6	5.0	27.92	36.92
							10.0	27.92	36.92
15	19°29′12″	92°07′30″	10/08/72	15:07	141.5	65.0	5.0	—	37.16
							10.0	28.50	37.16
							20.0	28.95	36.87
							40.0	28.01	37.13
16	19°20′12″	92°20′12″	10/08/72	13:50	253.9	36.9	5.0	28.70	37.02
							10.0	28.50	37.06
							20.0	28.30	37.05
17	19°13′00″	91°59′18″	10/08/72	12:30	201.6	25.0	5.0	28.32	36.08
							10.0	28.33	36.98
							20.0	28.25	37.05
18	19°03′12″	91°54′00″	10/08/72	11:03	216.0	21.0	5.0	28.20	37.08
							10.0	27.85	37.08
24	19°14′42″	91°48′30″	11/08/72	02:43	159.2	22.0	5.0	28.33	37.19
							10.0	28.33	36.98
							20.0	28.23	36.97
25	19°20′42″	91°51′54″	11/08/72	01:43	122.5	23.6	5.0	28.31	37.05
							10.0	28.21	37.02
							20.0	28.22	36.94

Table 1 (continued)

Station	Position		Date	Hour	Volume of water strained (m^3)	Depth of tow (m)	Physical and chemical date		
	Lat. N.	Long. W.					Depth (m)	Temp. (°C)	Salinity (ppt)
27	19°40′30″	92°02′06″	11/08/72	22:45	127.6	63.0	5.0	28.53	37.01
							10.0	28.54	37.06
							20.0	28.53	36.97
							40.0	28.23	36.87
29	20°10′30″	92°05′30″	12/08/72	06:58	144.8	70.0	6.0	28.42	37.12
							10.0	28.54	37.13
							14.0	28.42	37.13
							20.0	28.42	37.13
							40.0	28.11	37.10
30	20°02′00″	92°02′06″	12/08/72	05:45	138.2	62.0	6.0	28.42	37.14
							10.0	28.52	37.14
							14.0	28.42	37.14
							20.0	28.42	37.12
							40.0	28.21	36.95
31	20°53′12″	91°58′06″	12/08/72	02:20	142.1	50.0	6.0	28.45	37.08
							10.0	28.55	37.09
							14.0	28.55	37.10
							20.0	28.42	37.11
							40.0	25.31	36.93
32	19°44′00″	91°53′30″	11/08/72	23:27	154.2	54.2	6.0	28.75	36.92
							10.0	28.42	37.10
							14.0	28.02	37.03
							20.0	28.42	37.01
							40.0	28.03	36.99
33	19°37′00″	91°50′12″	11/08/72	20:43	154.5	45.0	6.0	28.43	36.93
							10.0	28.43	36.02
							14.0	28.43	36.99
							20.0	28.43	36.99
							40.0	28.87	36.88
35	19°18′48″	91°41′00″	11/08/72	15:29	158.7	21.6	6.0	28.50	36.97
							10.0	28.50	36.97
							14.0	28.30	36.97
							20.0	28.00	36.96
36	19°10′06″	91°36′48″	11/08/72	13:07	150.6	18.0	5.0	28.51	36.98
							10.0	28.51	36.98
							11.0	28.30	36.97
							16.5	28.21	36.95
41	19°16′30″	91°29′00″	11/08/72	14:18	187.5	16.2	5.0	27.32	36.96
							10.0	28.50	36.96
42	19°25′12″	91°33′06″	11/08/72	16:35	154.2	22.0	5.0	28.20	36.95
							10.0	28.60	36.92
							20.0	28.31	36.90
43	19°33′36″	91°37′00″	09/08/72	19:10	229.7	30.6	5.0	28.40	36.97
							10.0	28.45	36.97
							20.0	28.25	37.03
45	19°50′48″	91°45′24″	12/08/72	01:15	186.6	39.0	5.0	28.43	36.99
							10.0	28.33	37.02
							20.0	28.23	37.00
46	19°59′48″	91°49′48″	12/08/72	04:05	121.5	39.0	5.0	28.01	36.08
							10.0	28.02	36.97
							20.0	28.02	36.99
48	20°08′30″	91°43′00″	12/08/72	21:44	91.0	32.4	5.0	28.02	36.88
							10.0	28.02	36.82
							20.0	27.62	36.83
51	19°41′12″	91°31′12″	13/08/72	01:04	124.7	25.0	5.0	28.33	36.94
							10.0	28.33	—
							20.0	27.93	36.99

Table 1 (continued)

Station	Position		Date	Hour	Volume of water strained (m^3)	Depth of tow (m)	Physical and chemical date		
	Lat. N.	Long. W.					Depth (m)	Temp. (°C)	Salinity (ppt)
52	19°37′30″	91°26′30″	13/08/72	02:20	111.9	12.0	5.0	28.24	36.95
							10.0	28.22	36.94
53	19°25′12″	91°22′18″	13/08/72	03:15	65.9	15.0	5.0	28.23	36.94
55	19°06′48″	91°16′12″	13/08/72	05:15	78.8	10.8	5.0	28.23	37.33
57	19°22′12″	91°11′06″	14/08/72	12:30	148.0	14.0	5.0	28.71	36.83
							10.0	28.81	36.86
58	19°30′42″	91°14′12″	14/08/72	10:59	148.0	14.0	5.0	—	36.99
							10.0	—	36.93
59	19°37′18″	91°18′54″	14/08/72	10:09	183.5	25.0	5.0	28.21	36.87
							10.0	28.21	36.87
							20.0	25.85	36.90
60	19°47′30″	91°22′30″	14/08/72	06:24	123.2	23.4	5.0	28.13	36.91
							10.0	28.02	36.95
							20.0	27.31	—
61	19°55′30″	91°26′00″	14/08/72	04:50	164.1	30.0	5.0	28.02	36.90
							10.0	28.02	36.95
							20.0	26.51	36.90
72	19°45′00″	91°59′18″	13/08/72	12:09	192.4	14.8	5.0	28.61	37.00
							10.0	27.91	36.98
80	18°59′30″	92°58′00″	08/08/72	15:39	248.1	112.0	5.0	27.74	37.03
							10.0	28.03	36.01
							20.0	27.43	36.97
							40.0	23.70	36.86
							80.0	21.92	36.89
81	19°14′36″	92°53′06″	08/08/72	17:50	261.5	138.0	5.0	28.00	36.75
							10.0	27.40	36.72
							20.0	27.51	36.75
							40.0	27.51	37.04
							80.0	22.29	36.87
82	19°04′48″	92°50′12″	08/08/72	19:10	243.8	91.0	5.0	28.42	33.57
							10.0	27.31	36.95
							20.0	27.91	37.07
							40.0	23.27	36.87
							80.0	22.38	36.88
83	19°07′42″	92°41′12″	11/08/72	01:45	133.0	72.0	5.0	28.03	37.07
							10.0	27.91	37.08
							20.0	27.81	37.07
							40.0	23.85	36.86
84	19°16′30″	92°45′00″	11/08/72	03:06	277.7	135.0	5.0	27.51	36.99
							10.0	27.05	36.93
							20.0	27.51	36.96
							40.0	27.50	37.02
							80.0	21.99	36.98
85	19°26′42	92°39′12	11/08/72	06:47	298.5	167.0	5.0	28.43	37.09
							10.0	—	37.09
							20.0	28.22	37.15
							40.0	22.58	36.86
							80.0	18.64	36.96
86	19°17′00″	92°35′00″	11/08/72	06:47	174.7	99.0	5.0	27.90	37.13
							10.0	25.84	36.97
							20.0	26.85	37.13
							40.0	27.02	37.11
							80.0	28.01	36.07
87	19°08′42″	92°33′30″	11/08/72	08:40	258.3	54.0	5.0	—	36.99
							10.0	28.22	37.00
							20.0	28.20	37.02
							40.0	23.10	37.06

Table 1 (continued)

Station	Position		Date	Hour	Volume of water strained (m^3)	Depth of tow (m)	Physical and chemical date		
	Lat. N.	Long. W.					Depth (m)	Temp. (°C)	Salinity (ppt)
90	19°21′30″	92°26′00″	11/08/72	18:04	167.1	84.0	5.0	28.50	37.03
							10.0	—	37.05
							20.0	28.40	37.05
							40.0	28.00	37.09
							80.0	21.91	—
92	19°42′42″	92°24′42″	10/08/72	24:18	244.8	140.0	5.0	28.32	36.98
							10.0	27.00	37.11
							20.0	28.32	37.14
							40.0	28.22	37.21
							80.0	22.60	37.15
93	19°32′00″	92°19′48″	09/08/72	19:43	180.1	86.4	5.0	28.51	37.12
							10.0	30.44	37.12
							20.0	28.41	37.15
							40.0	28.31	37.16
							80.0	21.90	36.86
94	19°23′24″	92°16′18″	10/08/72	02:41	127.3	39.0	5.0	28.31	37.04
							10.0	28.21	36.86
							20.0	28.22	37.05
95	19°37′00″	92°13′00″	10/08/72	16:53	181.5	108.0	5.0	28.50	37.14
							10.0	—	37.13
							20.0	28.40	37.15
							40.0	28.21	37.15
							80.0	22.60	37.15
96	19°51′06″	92°29′36″	10/08/72	18:53	173.4	90.0	5.0	—	—
							10.0	—	—
							20.0	33.29	36.95
							40.0	—	—
							80.0	28.2	36.97

Table 2

Relative abundance (number of larvae per 10 m^2 of sea surface) of the Scombridae captured during the COSMA 16-72 cruise. Positive stations are stations at which scombrid larvae were collected.

Species	Number of positive stations	Number per 10 m^2			Percentage of total
		Total	Daytime	Nighttime	
Frigate tuna	37	4473	370	4103	7
Thunnus spp.	36	651	180	471	11
Little tunny	21	417	113	304	7
Bigeye tuna	6	120	51	69	2
Blackfin tuna	2	58	—	58	1
King mackerel	8	35	16	19	1
Spanish mackerel	2	31	27	4	1
Yellowfin tuna	2	24	24	—	1
Skipjack tuna	1	14	14	—	1

species, the little tunny, the bigeye tuna, and the blackfin tuna, respectively.

A total of 4473 frigate tuna larvae were captured per 10 m^2 of sea surface, with a mean of 86 over 37 positive sampling stations. Significantly more frigate tuna larvae were caught during the nighttime than in the daytime ($P<0.05$) (Table 2). The frigate tunas captured ranged from 2.00 to 7.75 mm; those smaller than 2.25 mm were under represented in the samples, and were eliminated from further analysis. Frigate tunas in the 2.76–3.25 mm

Table 3

Absolute abundance by standard length (mm) of frigate tuna larvae captured during the COSMA 16-72 cruise. (The total for each positive station = C_j [Equation 1] and the total for each length class = P [Equation 7].)

	Standard length range (midpoint)											
Station	2.25–2.75 (2.50)	2.76–3.25 (3.00)	3.26–3.75 (3.50)	3.76–4.25 (4.00)	4.26–4.75 (4.50)	4.76–5.25 (5.00)	5.26–5.75 (5.50)	5.76–6.25 (6.00)	6.26–6.75 (6.50)	6.76–7.20 (7.0)	7.25–7.75 (7.50)	Total (C_j)
4	3	—	—	—	—	—	—	—	—	—	—	3
9	—	—	—	—	—	1	—	—	—	—	—	1
10	6	1	—	—	—	—	—	—	—	—	—	7
15	—	—	—	—	—	—	—	2	—	—	—	2
16	—	17	1	—	—	—	—	—	1	—	—	19
17	—	—	—	—	—	—	—	1	—	—	—	1
18	—	1	—	—	—	—	—	—	—	—	—	1
24	—	—	—	—	—	1	—	—	—	—	—	1
25	5	1	—	—	—	—	—	—	—	—	—	6
27	5	11	3	—	—	—	—	—	—	—	—	19
29	—	—	—	1	—	—	—	—	—	—	—	1
30	—	—	—	—	—	—	—	1	—	—	—	1
31	21	14	5	6	2	3	1	—	—	—	—	52
32	—	—	4	10	3	2	—	—	—	—	—	19
33	—	—	—	2	1	1	—	—	—	—	—	4
36	—	5	—	—	—	—	—	—	—	—	—	5
42	—	—	—	1	1	—	—	—	1	—	—	3
43	18	26	1	1	—	—	—	—	—	—	—	46
45	—	—	—	1	1	1	—	—	—	—	—	3
46	—	—	1	—	—	—	—	—	—	—	—	1
48	1	1	—	—	—	—	—	—	—	—	—	2
51	—	—	—	—	—	2	—	1	—	—	—	3
53	4	—	1	—	1	1	1	—	1	—	—	9
60	20	6	1	—	—	—	—	—	—	—	—	27
61	11	7	1	—	—	—	—	—	—	—	—	19
81	—	—	—	—	—	2	—	—	—	—	—	2
82	—	—	—	—	—	2	—	—	—	—	—	2
83	2	6	3	—	—	4	2	—	—	—	—	17
84	10	13	3	—	—	—	—	—	—	—	—	26
85	—	5	6	2.5	2	—	—	—	—	—	1	39
86	—	—	—	—	—	—	—	1	—	—	—	1
87	4	5	1	1	—	—	—	—	—	—	—	11
90	6	6	1	—	—	—	—	—	—	—	—	13
92	—	—	—	1	—	—	—	1	—	—	—	2
93	—	—	—	6	3	7	4	1	—	—	—	21
94	391	616	28	2	—	—	—	—	—	—	—	137
95	—	—	—	—	—	1	—	—	—	—	—	1
Total	507	741	60	57	14	28	8	8	3	0	1	1427

length class were the most abundant (Table 3). Sampling Stations 94, 85, and 31 had the greatest standardized densities (Fig. 2), with 3173, 218, and 183, respectively, per 10 m^2 of sea surface (Table 4). These stations were located between 70 and 90 km (40 and 50 nautical miles [nmi]) from Puerto Frontera and Punta Frontera.

The little tunny was the second most abundant species (Table 2). Its larval distribution pattern indicated that the adults spawned in areas greater than 54 km (30 nmi) from the coast (Fig. 3). In contrast, some frigate tuna larvae were found somewhat closer to the coastline. Maximum densities were obtained at Stations 93 and 32, with 81 and 88 larvae per 10 m^2 of sea surface, respectively. These stations were located 95 and 117 km from Punta Frontera and Ciudad del Carmen. Catches of little tunny larvae were significantly higher ($P<0.05$) at night than in the daytime (Table 2). Sizes ranged from 3.0–12.5 mm, and the 3.76–4.25 mm length class was the modal class.

The third most abundant species was the bigeye tuna (Table 2) at Stations 30 and 31 located 144–189 km (80–105 nmi) from Atasta and Campeche (Fig. 4). Standardized densities at these stations averaged 25 and 50 larvae, respectively, per 10 m^2 of sea surface. Larval sizes ranged from 3.0–7.0 mm, with most individuals being in the

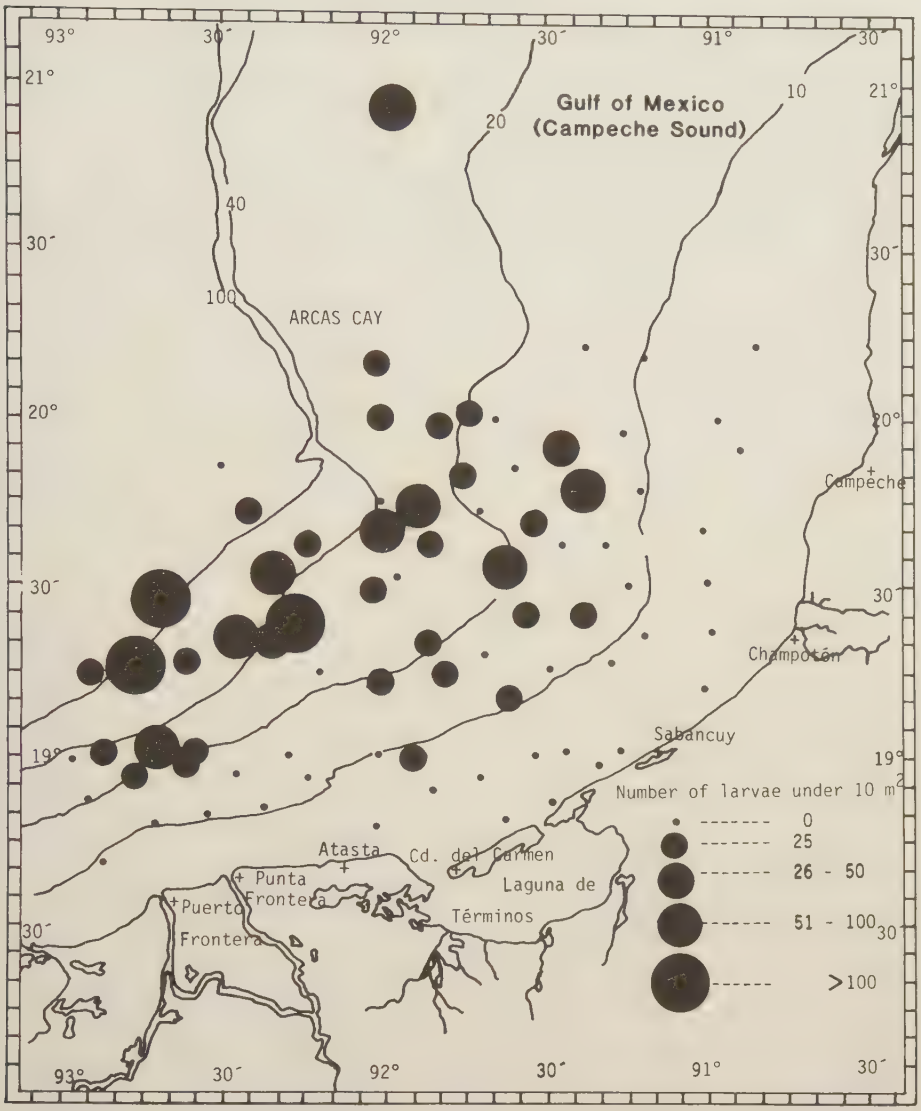

Figure 2
Distribution and standardized abundance of frigate tuna larvae during the COSMA 16-72 cruise. Depth contours are in fathoms.

3.76–4.25 mm class. No significant difference was observed between diurnal and nocturnal capture rates.

Blackfin tuna larvae were captured at only two stations, 92 and 27 (Fig. 4). These stations were located about 115 and 106 km (62 and 57 nmi) from Punta Frontera and Atasta. Numbers captured did not exceed 30 larvae per 10 m^2 of sea surface. The larval sizes ranged from 6.0–11.5 mm, with specimens in the 5.76–6.25 mm class predominating. Capture of this species took place only in nocturnal tows (Table 2).

A total of 35 king mackerel, *Scomberomorus cavalla*, larvae were caught, with a maximum of 10 larvae per 10 m^2 of sea surface at Station 81 located 72 km (40 nmi) from Puerto Frontera (Fig. 4). Larvae were captured at stations located as close as 36 km (20 nmi) from the coastline. King mackerel larvae ranged from 2.5–11.0 mm, with the 4.76–5.25 mm length class predominating. No significant difference was found between diurnal and nocturnal catches.

Spanish mackerel, *S. maculatus*, larvae were found at Stations 82 and 80 located 48–50 km (27–28 nmi) from Puerto Frontera (Fig. 5). A total of 31 larvae were sampled. Catches were significantly higher in the daytime than at night ($P<0.05$). The maximum density was 27 larvae per 10 m^2 of sea surface at Station 80. Sizes ranged from 8.0–15.5 mm, with no length class predominating. Judging by the size of the specimens captured, spawning took place a considerable time before sampling.

Yellowfin tuna larvae measuring 3.0–10.0 mm were captured at Stations 95 and 30 located at 104 and 144 km (58 and 80 nmi) from Punta Frontera and Atasta (Fig. 5). Yellowfin larvae were caught only in daytime tows (Table 2).

The skipjack tuna, *Katsuwonus pelamis*, was the least abundant species in the samples (Table 2). The only positive station was Station 15 located 86 km (40 nmi) from Atasta (Fig. 5). The larvae captured ranged from 6.0–7.0

Table 4

Relative abundance (number per 10 m^2 of sea surface [N_j, Equation 1]) by standard length (mm) of frigate tuna larvae captured during the COSMA 16-72 cruise. The standard haul factor (SHF) was obtained by the method of Kramer et al. (1972).

		Standard length range (midpoint)											
Station	S.H.F.	2.25–2.75 (2.50)	2.76–3.25 (3.00)	3.26–3.75 (3.50)	3.76–4.25 (4.00)	4.26–4.75 (4.50)	4.76–5.25 (5.00)	5.26–5.75 (5.50)	5.76–6.25 (6.00)	6.26–6.75 (6.50)	6.76–7.20 (7.0)	7.25–7.75 (7.50)	Total
4	0.94	2.82	—	—	—	—	—	—	—	—	—	—	2.82
9	2.95	—	—	—	—	—	2.95	—	—	—	—	—	2.95
10	1.84	11.04	1.84	—	—	—	—	—	—	—	—	—	12.88
15	4.59	—	—	—	—	—	—	—	9.18	—	—	—	9.18
16	1.41	—	23.93	1.41	—	—	—	—	—	1.41	—	—	26.79
17	0.81	—	—	—	—	—	—	—	0.81	—	—	—	0.81
18	0.97	—	0.97	—	—	—	—	—	—	—	—	—	0.97
24	1.38	—	—	—	—	—	1.38	—	—	—	—	—	1.38
25	1.92	9.60	1.92	—	—	—	—	—	—	—	—	—	12.52
27	4.94	24.70	54.34	14.82	—	—	—	—	—	—	—	—	93.86
29	4.83	—	—	—	4.83	—	—	—	—	—	—	—	4.83
30	4.48	—	—	—	—	—	—	—	4.48	—	—	—	4.48
31	3.51	73.71	49.14	17.55	21.06	7.02	10.53	3.51	—	—	—	—	182.52
32	3.50	—	—	14.00	35.00	10.50	7.00	—	—	—	—	—	66.50
33	2.91	—	—	—	5.82	2.91	2.91	—	—	—	—	—	11.64
36	1.19	—	5.95	—	—	—	—	—	—	—	—	—	5.95
42	1.43	—	—	—	1.43	1.43	—	—	—	1.43	—	—	4.29
43	1.33	23.94	34.58	1.33	1.33	—	—	—	—	—	—	—	61.18
45	1.87	—	—	—	1.87	1.87	1.87	—	—	—	—	—	5.61
46		—	—	3.21	—	—	—	—	—	—	—	—	3.21
48	3.56	3.56	3.56	—	—	—	—	—	—	—	—	—	7.12
51	2.00	—	—	—	—	—	4.00	—	2.00	—	—	—	6.00
53	2.27	9.08	—	2.27	—	2.27	2.27	2.27	—	2.27	—	—	20.43
60	1.90	38.00	11.40	1.90	—	—	—	—	—	—	—	—	51.30
61	1.83	20.13	12.81	1.83	—	—	—	—	—	—	—	—	34.77
81	5.27	—	—	—	—	—	10.54	—	—	—	—	—	10.54
82	3.73	—	—	—	—	—	7.46	—	—	—	—	—	7.46
83	5.41	10.82	32.46	16.23	—	—	21.64	10.82	—	—	—	—	91.97
84	4.86	48.60	63.18	14.58	—	—	—	—	—	—	—	—	126.36
85	5.59	—	27.95	33.54	139.75	11.18	—	—	—	—	—	5.59	218.01
86	5.66	—	—	—	—	—	—	—	5.66	—	—	—	5.66
87	2.10	8.40	10.50	2.10	2.10	—	—	—	—	—	—	—	23.10
90	5.03	30.18	30.18	5.03	—	—	—	—	—	—	—	—	65.39
92	5.72	—	—	—	5.72	—	—	—	5.72	—	—	—	11.44
93	4.80	—	—	—	28.80	14.40	33.60	19.20	4.80	—	—	—	100.80
94	3.06	1196.46	1884.96	85.68	6.12	—	—	—	—	—	—	—	3173.22
95		—	—	—	—	—	5.95	—	—	—	—	—	5.95
Total		1511.04	2249.71	215.48	253.83	51.58	112.10	35.80	32.65	5.11	0	5.59	4472.89

mm. Skipjack larvae were caught only in daytime tows (Table 2).

The abundance (P_i) of frigate tuna larvae calculated by 0.5 mm length classes using equations 2 and 3 varied between 0.166×10^9 and 48.154×10^9 larvae in the area covered by the positive stations (Table 5). Ages of the larvae corresponding to the midpoints of each length class were estimated to be 3.7–22.0 days.

Larval production (P_a, Equation 4) during the spawning season for the 2.5-mm length class was 1.731×10^{12} larvae (Table 5). Residence time was 3.3 d for larvae spawning that size class. P_{adj} (Equation 6) was 6.227×10^{12} larvae.

Reproductive Biomass

The biomass of reproductive frigate tuna adults was calculated using the P_{adj} estimate (above), F_r of 76 eggs $\cdot g^{-1}$, and K of 0.5 in Equation 6. The reproductive biomass was estimated to be 163868 mt based on abundance of the 2.5-mm length class.

Larval Mortality Rate

Absolute abundance of the frigate tuna larvae decreased exponentially with age (Fig. 6). P values for each length

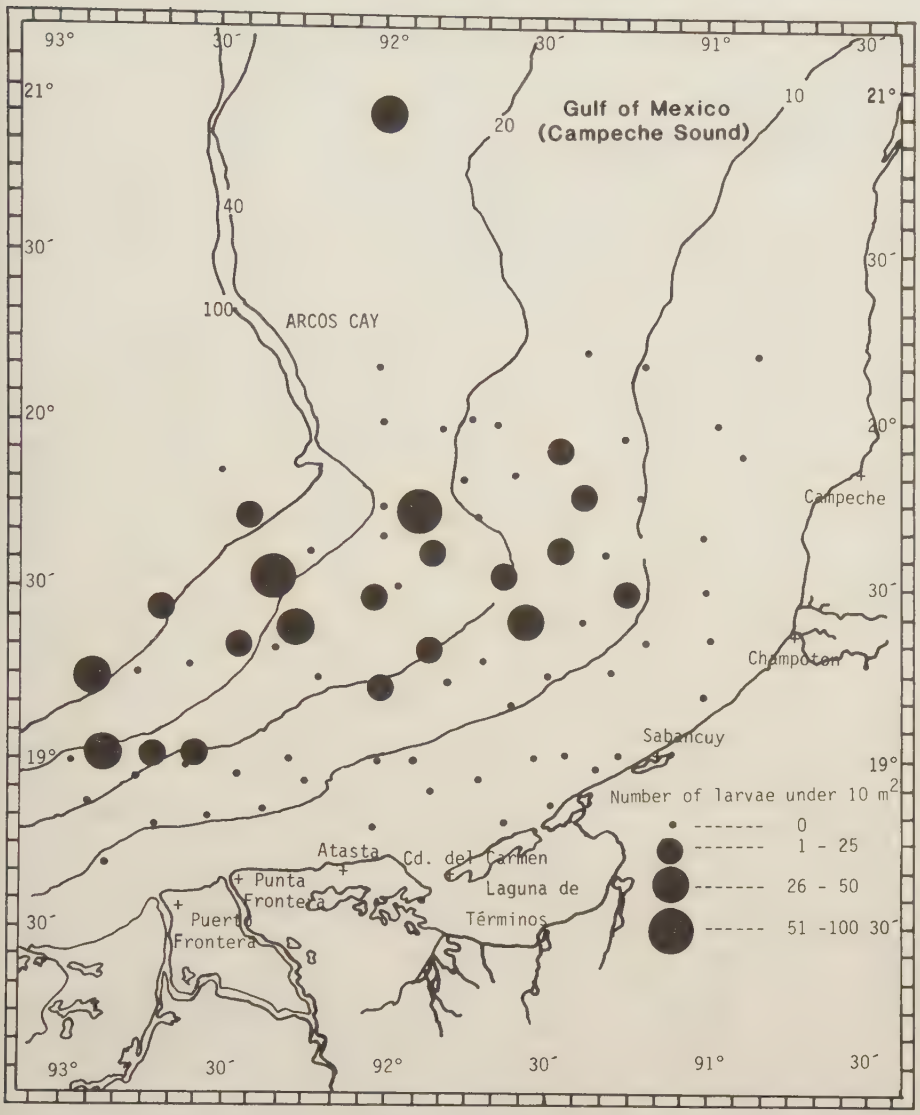

Figure 3
Distribution and standardized abundance of little tunny larvae during the COSMA 16-72 cruise. Depth contours are in fathoms.

class (Table 3) and the ages corresponding to the midpoints of the length classes (Table 5) fitted to Equation 7 yielded the equation given in Figure 6. The daily mortality coefficent, M, was 0.346.

Discussion and Conclusions

Identification of larval scombrids is not unambiguous (Richards and Potthoff 1973; Graves et al. 1988). The pigmentation pattern present on the frigate tunas in this study suggests that they are *Auxis thazard*. Nevertheless, owing to the difficulty in distinguishing the frigate tunas as larvae (Uchida 1981), our results are presented for the *Auxis* spp. complex. There is a conflict in the literature concerning the diagnostic pigmentation of larval *Thunnus atlanticus* (Juárez 1972; Richards and Potthoff 1973). However, we are confident of the species identifications in this study because the *Thunnus* spp. were cleared and stained, and the number of vertebrae were counted.

The distribution and abundance of larval scombrids in the study area suggest that Campeche Sound is an important tuna spawning area, especially for the frigate tunas and the little tunny. It is noteworthy that, although low in abundance, the presence of larvae of the larger tunas, such as yellowfin and bigeye, indicates that these species also spawn in the area. Although it has been reported that the frigate tunas spawn in almost the entire Gulf of Mexico (Idyll and de Sylva 1963), the frigate tunas and the little tunny are found mainly in waters adjacent to land masses (Williams 1963; Juárez 1974). Larval distribution and abundance of the Scombridae in the Gulf of Mexico reported by Juárez (1974, 1976) and Ramírez and Ornelas (in press) have shown that spawning activity is lower in oceanic than coastal waters. We believe that this is related to the temperature and productivity of the area, both

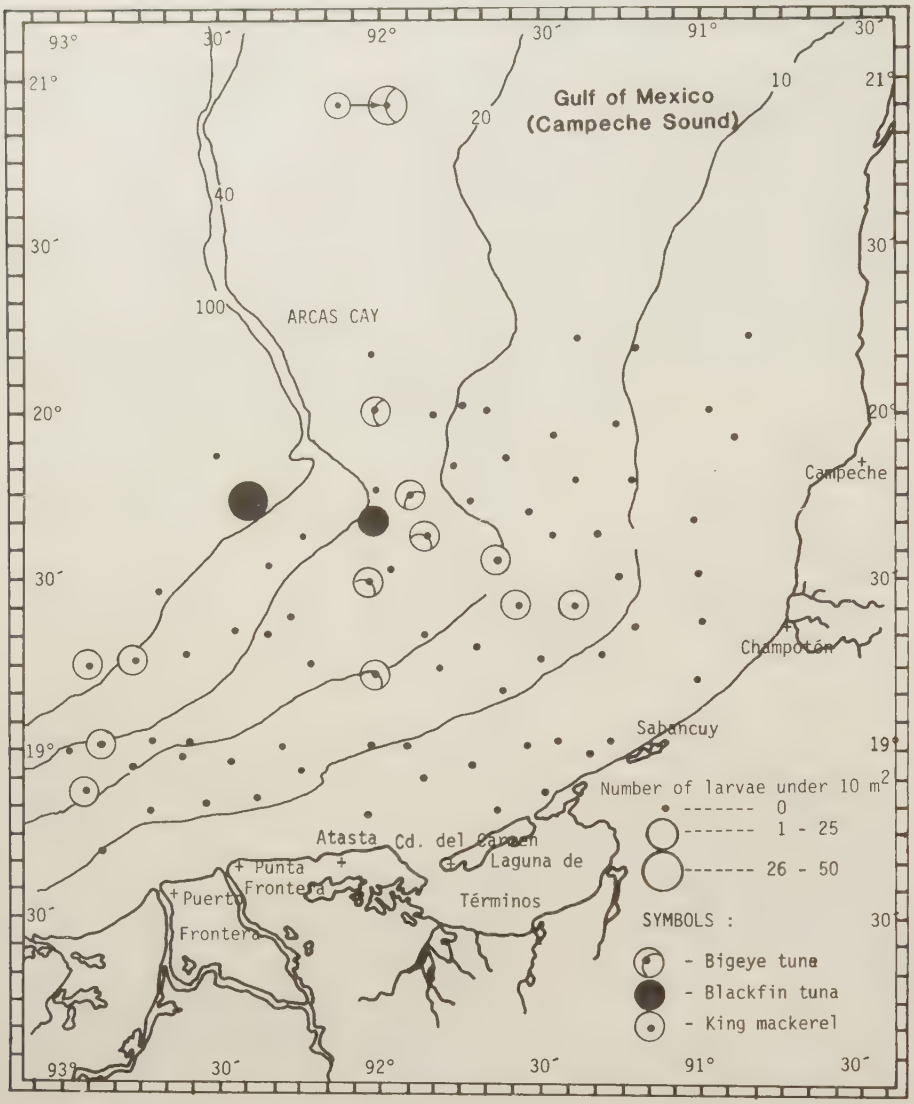

Figure 4
Distribution and standardized abundance of bigeye tuna, blackfin tuna, and king mackerel larvae during the COSMA 16-72 cruise. Depth contours are in fathoms.

important factors in determining breeding areas. It is important to relate future ichthyoplankton studies to information on current dynamics, physical-chemical conditions, hydrological conditions, and biological productivity, and to obtain information on the role of each species in the trophicdynamics of the ecosystem.

The extent of the frigate tunas' spawning area in the Gulf of Mexico is not known, and the population boundaries would be difficult to determine. Although the COSMA 16-72 cruise was not long enough to give an adequate representation of larval production over the spawning season, we consider these data to be important for designing a future survey that would yield an adequate representation of the production dynamics over population sectors.

Our estimate of 163868 t of frigate tuna reproductive biomass suggests that they are a potential fishery resource in the region. In other countries, such as India and Ceylon in the Indian Ocean, this species is considered to be an important fishery resource, and it is utilized in the same form as other small tunas (Williams 1963; Juárez 1976). Our large spawning population estimate is supported by the fact that the Campeche Sound is a highly productive area where the frigate tunas suffer no significant exploitation. On the other hand, our estimates may be low for the following reasons. The portion of the Campeche Sound that was sampled is probably at the fringes of the populations' spawning area in the Gulf of Mexico. In using larval abundance data for computing spawning biomass and in not accounting for mortality between recently spawned eggs and the larval stage, we have computed only a fraction of the initial egg production which is directly related to spawning stock. Egg mortality of pelagic fishes is typically high, although the gestation period is likely short at these temperatures (Table 1). This information will be improved when more is known of the duration of spawning, fecun-

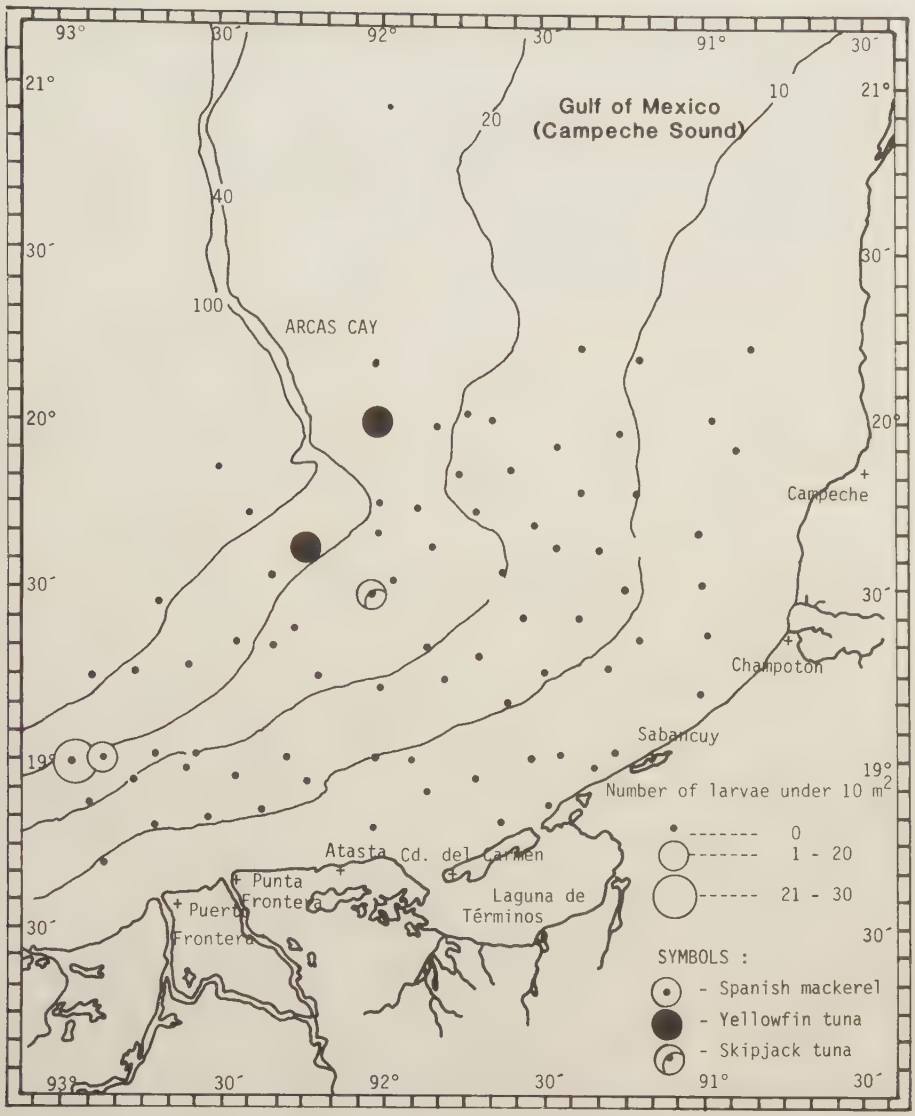

Figure 5
Distribution and standardized abundance of Spanish mackerel, yellowfin tuna, and skipjack tuna larvae during the COSMA 16-72 cruise. Depth contours are in fathoms.

Table 5
Abundance by standard length (mm) of frigate tuna larvae for the total area represented by positive stations (P_i, Equation 3), total larval production (P_a, Equation 4) throughout the spawning season, and the reproductive biomass estimate (B_a, Equation 6).

Length Class (SL mm)	Range Midpoint	P_i (no. × 10^9)	Age (d)	P_a (no. × 10^{12})	B_a (t)
2.25–2.75	2.5	31.741	3.7	—	—
2.76–3.25	3.0	48.154	6.8	—	—
3.26–3.75	3.5	9.028	9.3	—	—
2.76–4.25	4.0	7.478	11.6	—	—
4.26–4.75	4.5	1.407	13.5	—	—
4.76–5.25	5.0	3.548	15.3	—	—
5.26–5.75	5.5	0.980	16.9	—	—
5.76–6.25	6.0	1.025	1.83	—	—
6.26–6.75	6.5	0.166	19.6	—	—
7.26–7.75	7.5	0.192	22.0	—	—
			Total	1.73	163868

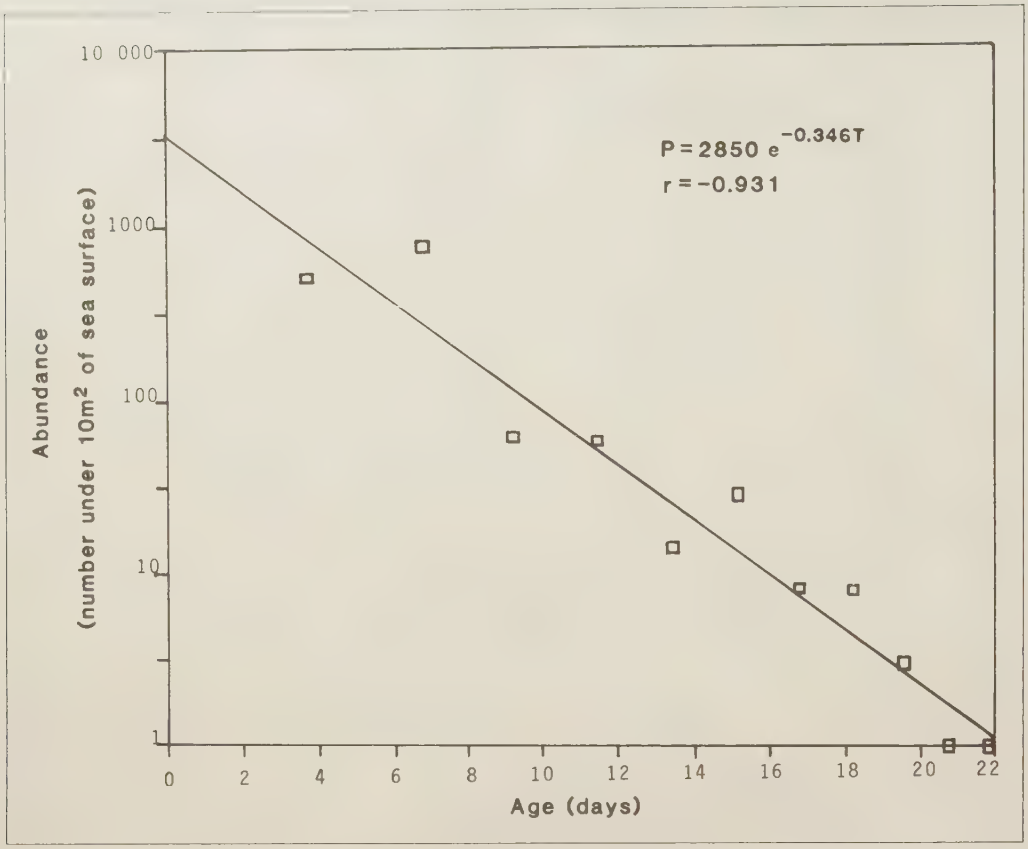

Figure 6
Absolute abundance of frigate tuna larvae (*P*, Table 3) versus age corresponding to the midpoints of each size class (Table 5).

dity, sex ratios, growth rates, and mortality during the egg and larval stages.

Acknowledgments

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Abundance and Distribution of Fish Larvae in the Channel Area of the Patos Lagoon Estuary, Brazil

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ABSTRACT

Distribution and abundance of fish larvae in the channel area of the Patos Lagoon, Brazil are reported. The Patos Lagoon is a shallow coastal lagoon with a very narrow connection with the Atlantic Ocean. Its southernmost region, characterized by a very dynamic estuary, was the site of 32 ichthyoplankton surveys conducted at 5 stations from April 1981 to March 1983. Samples were taken at 3 depth levels (surface, mid-water and bottom) and results indicated that larval density and distribution were associated with temperature. Larvae occurred year round and at all stations, but were most abundant and diverse during spring and summer with mean densities of 61/100 m^3 and 189/100 m^3, respectively. However, this distribution was sometimes altered by meteorological conditions prevailing in the estuary. Twenty families of fishes were represented, including 27 taxa, 19 of which were identified to species. The three most abundant taxa overall were *Micropogonias furnieri*, *Brevoortia pectinata*, and *Lycengraulis* sp., whose larvae accounted for 22.9, 22.6, and 20% of the total, respectively. *Parapimelodus valenciennis*; Blennidae; *Trichiurus lepturus*; *Gobiesox strumosus*; *Paralonchurus brasiliensis*; *Macrodon ancylodon*; *Paralichthys* sp.; Atherinidae; *Gobiosoma parri*; and *Menticirrhus* spp. had relative abundances between 1 and 5%.

Introduction

Estuaries and coastal waters play an important role in the life cycles of various marine organisms. They provide an abundance of food and protection from predators for larval and juvenile fishes which use these areas as nursery grounds (Pearcy and Myers 1974; Chao and Musick 1977; Misitano 1977; Weinstein 1979; Weiss 1981; Castello 1986). Many marine fish species inhabit regions close to estuaries and rivers. Their eggs and larvae are transported into these areas where they develop and grow. In the North Atlantic, 70% of commercially important fish species spend part of their life cycle in or near estuaries (McHugh 1966, 1967; Clark 1967). In Mexico, Yañez-Arancibia (1978) reported that 80% of the coastal ichthyofauna was related to coastal lagoons or areas influenced by them. In addition to these marine species, there are some groups that have their entire life cycles confined to estuarine areas (Weiss 1981; Chao et al. 1982a).

According to Flores-Coto et al. (1983), the association between ichthyofauna and estuarine environments cannot be completely understood without ichthyoplankton studies which provide information about the early life histories of these organisms. Despite their importance, only a few surveys have been conducted in Brazil to study the relationship between estuarine environments and the development of fish eggs and larvae (Phonlor 1975; Castello 1976, 1977, 1978; Weiss and Krug 1977; Sinque 1980; Weiss 1981; Muelbert 1986).

The Patos Lagoon, located in the southernmost state of Brazil, is the largest coastal lagoon of South America, covering an area of 10360 km^2. Its southern region (900 km^2) is characterized by a very dynamic estuary (Fig. 1). Its dynamic characteristics are determined by its topography and prevailing meteorological conditions, since the tidal range within the estuary is limited to a low diurnal tidal amplitude (mean of 0.47 m). Most of the estuarine area is very shallow (mean depth of 2 m), and a channel in its center (mean depth of 15 m) leads to a very narrow inlet (750 m) connecting the estuary to the Atlantic Ocean. Wind pattern and precipitation in the highlands drained by the lagoon determine the salinity regime of the estuary

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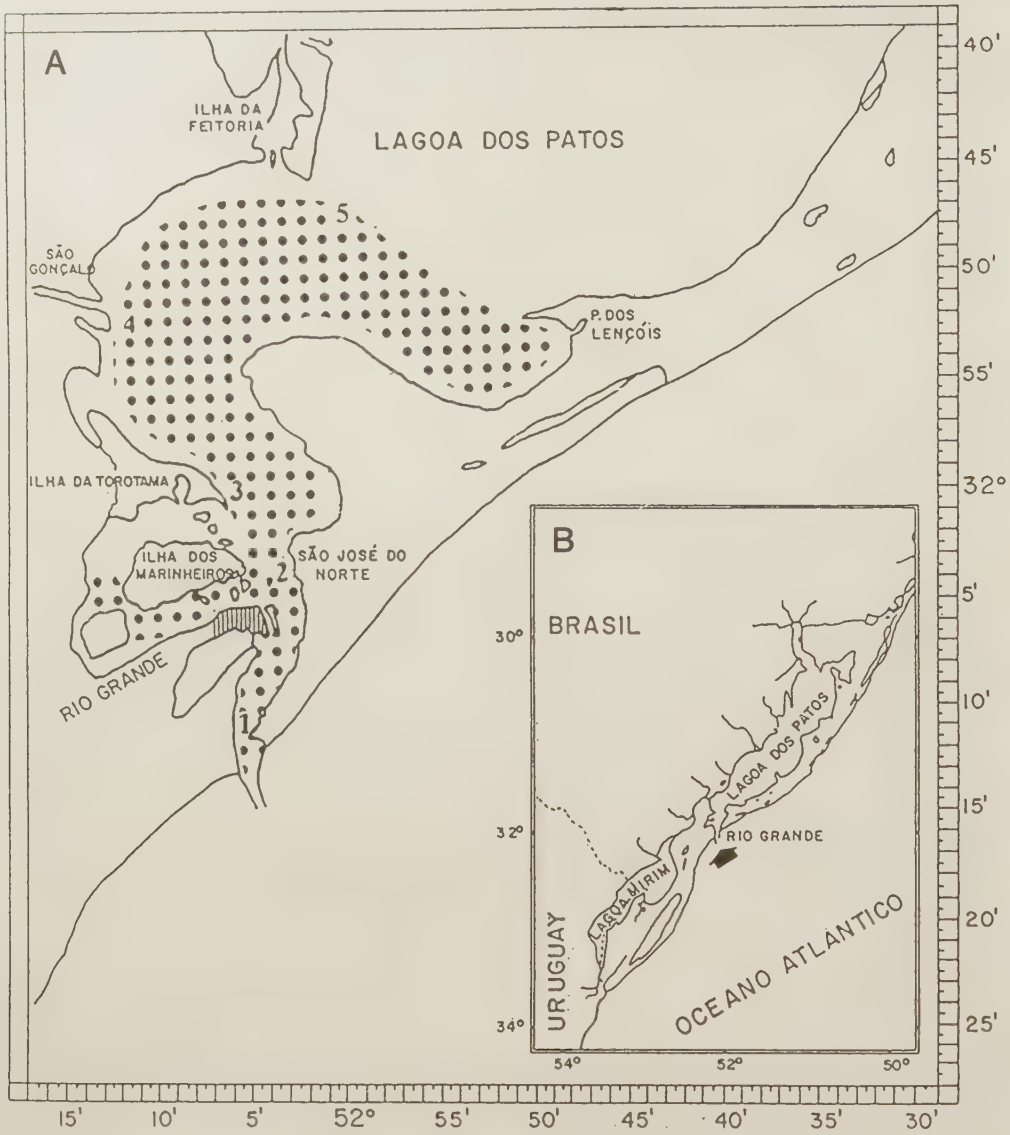

Figure 1
Study area and location of the sampling stations. Dotted area represents estuarine region of the Patos Lagoon.

(Castello and Möller 1978). Southerly winds are associated with salt water intrusion whereas northerly winds are related to oligohaline conditions (Costa et al. 1988).

Chao et al. (1982b) cited 110 estuarine and marine fish species inhabiting the estuary and the adjacent coastal waters of the Patos Lagoon. *Brevoortia pectinata*, *Micropogonias furnieri*, *Cynoscion striatus*, and *Macrodon ancylodon* are commercially important species whose larvae use the Patos Lagoon estuary as a nursery ground (Weiss 1981).

In this paper, we present results on abundance and distribution of fish larvae in the channel of the Patos Lagoon estuary. The study was restricted to the channel area of the estuary to account for the influence of salt water intrusion and freshwater run-off in the assemblage of fish larvae.

Materials and Methods

Fish eggs and larvae were collected during 32 ichthyoplankton surveys at five sampling stations in the Patos Lagoon estuary from April 1981 to March 1983 (Fig. 1; Table 1). The sampling stations were distributed along the channel area of the estuary from its connection with the ocean to its most interior limit. Stations 1, 2, and 3 were sampled at surface, mid-water and bottom depths, whereas only surface and bottom were sampled at stations 4 and 5, which were shallower. All five stations were sampled on the same day.

A 61-cm conical net without a closing system was used to take the samples. Owing to the high concentration of

Table 1

Absolute and relative density of fish larvae, temperature, and salinity (Mean ± SE) for the entire study.

Survey	Date	Season	Temperature (°C)	Salinity (ppt)	Larval density	
					(N/100m^3)	(%)
1	06/04/81	Autumn	22.5 ± 0.3	18.9 ± 2.0	44.3 ± 9.4	1.72
2	01/06/81	Autumn	18.5 ± 0.03	8.1 ± 2.0	6.4 ± 1.0	0.25
3	19/06/81	Autumn	15.1 ± 0.4	25.2 ± 0.8	24.0 ± 10.0	0.93
4	16/07/81	Winter	15.3 ± 0.3	18.9 ± 3.0	34.0 ± 9.0	1.32
5	31/07/81	Winter	16.3 ± 0.3	2.2 ± 0.4	40.3 ± 8.9	1.57
6	20/08/81	Winter	18.4 ± 0.4	8.4 ± 2.0	18.7 ± 4.5	0.73
7	28/08/81	Winter	19.6 ± 0.5	16.3 ± 2.9	11.4 ± 2.2	0.44
8	08/09/81	Winter	19.6 ± 0.4	1.2 ± 0.5	34.0 ± 10.0	1.32
9	22/09/81	Winter	18.7 ± 1.2	3.2 ± 1.8	9.3 ± 1.7	0.36
10	16/10/81	Spring	21.7 ± 1.0	8.0 ± 3.0	8.0 ± 2.2	0.31
11	11/11/81	Spring	24.3 ± 1.5	12.6 ± 3.1	91.8 ± 39.5	3.57
12	25/11/81	Spring	24.0 ± 0.6	6.9 ± 2.0	44.5 ± 7.4	1.73
13	04/12/81	Spring	21.2 ± 0.8	19.5 ± 2.0	30.4 ± 9.6	1.18
14	23/12/81	Summer	22.6 ± 0.3	23.7 ± 2.8	202.3 ± 39.1	7.87
15	11/01/82	Summer	21.4 ± 0.4	27.2 ± 3.0	145.9 ± 19.4	5.68
16	22/01/82	Summer	23.3 ± 1.2	22.1 ± 4.0	474.4 ± 66.6	18.46
17	08/02/82	Summer	23.9 ± 1.1	31.5 ± 1.5	79.0 ± 23.8	3.08
18	02/04/82	Autumn	23.8 ± 0.2	32.2 ± 1.0	84.8 ± 16.4	3.30
19	13/05/82	Autumn	20.1 ± 0.3	27.5 ± 2.0	5.6 ± 1.4	0.22
20	01/06/82	Autumn	15.8 ± 0.4	26.4 ± 2.0	2.0 ± 0.8	0.08
21	25/06/82	Winter	13.7 ± 0.6	9.6 ± 0.5	1.1 ± 0.4	0.04
22	09/08/82	Winter	14.5 ± 0.4	1.5 ± 0.5	156.0 ± 41.9	6.07
23	30/08/82	Winter	16.5 ± 0.7	3.7 ± 1.8	118.8 ± 24.7	4.62
24	06/09/82	Winter	16.0 ± 0.0	12.2 ± 3.0	44.0 ± 17.9	1.71
25	20/09/82	Winter	16.2 ± 0.4	13.2 ± 2.8	19.0 ± 17.5	0.74
26	13/10/82	Spring	14.8 ± 0.3	21.9 ± 2.8	29.7 ± 10.8	1.16
27	17/11/82	Spring	19.1 ± 0.3	0.0 ± 0.1	72.2 ± 14.0	2.81
28	13/12/82	Spring	24.3 ± 0.3	2.0 ± 1.8	140.4 ± 22.9	5.47
29	23/12/82	Summer	24.6 ± 0.8	0.3 ± 0.7	69.5 ± 10.9	2.70
30	07/01/83	Summer	22.8 ± 0.6	1.7 ± 1.5	176.1 ± 43.1	6.85
31	21/01/83	Summer	23.9 ± 0.8	24.9 ± 3.0	169.4 ± 35.9	6.59
32	10/02/83	Summer	23.4 ± 2.1	9.7 ± 3.6	181.5 ± 51.5	7.06

suspended material, a 500-μm mesh size was used to minimize clogging of the net. Tows, lasting three minutes each, were taken during daylight hours at a speed of 1 m/s against the water current. This procedure resulted in an overestimation of the bottom and mid-water samples of approximately 10 and 5%, respectively. A self-constructed digital flowmeter (identical to General Oceanics Model 2030) was placed in the mouth of the net to estimate volume filtered. Salinity values were obtained using an American Optical refractometer and expressed as ppt (parts per thousand). Water temperature, recorded in degrees Centigrade, was obtained by thermometer. Water samples were collected with a bucket from the surface and with a modified Niskin bottle from mid-water and bottom. All sampled material was preserved with 5% buffered formalin and processed in the laboratory. Fish eggs and larvae were sorted and counted using a binocular dissecting microscope and their densities were standardized to 100 m^3 of water filtered. Larvae and egg identification was done following Weiss (1981), and determined to the lowest taxonomic level possible. Standard length was measured for the most important species, *Brevoortia pectinata*, *Lycengraulis* sp., and *Micropogonias furnieri*, with an ocular micrometer. Seasonal designations were based on the solar calendar for the Southern Hemisphere. Only the results regarding fish larvae will be addressed in this paper.

A three-way analysis of variance (ANOVA) (Kim and Kohout 1975) was used to assess the effect of season, sampling station, depth strata, and the interactions of these factors on the distribution of temperature, salinity, and larval density. This analysis was combined with the Multiple Comparisons Test of Scheffé ($P<0.05$) to determine the significant differences observed in the spatial and temporal distribution of the dependent variables. Normality of the variables was obtained with the use of the following mathematical transformation of the raw data: salinity and

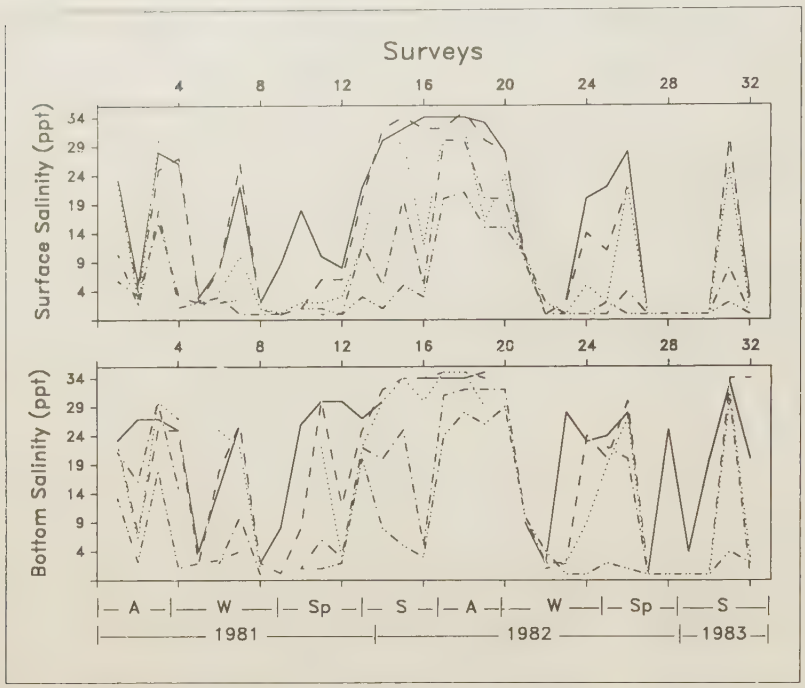

Figure 2
Distribution of salinity (ppt) at each station for the 32 surveys. (———) station 1; (- - -) station 2; (· · · · ·) station 3; (- · - · -) station 4; and (- · · - · · -) station 5. A = Autumn; W = Winter; Sp = Spring; S = Summer.

fish larval density were transformed with the expression $y = \ln(x \pm 1)$. Normality was confirmed with the use of Student's t test ($t<0.025$) for the values of asymmetry and kurtosis of the transformed variable, and homogeneity of variance was tested using Bartlett-Box F statistics ($P<0.05$) (Sokal and Rohlf 1981).

Results and Discussion

Salinity and Temperature

During the study period the mean ($\bar{x}$) salinity (for all sample stations and depths combined) ranged from 0.0 to almost 35.0 ppt and exhibited a seasonal trend (Fig. 2; Table 1). An increase in salinity values was observed from spring to autumn, the period of maximum salinity. After autumn, the values began to decrease and reached minimal levels in winter (Table 1). However, this pattern was not constant, as shown by sudden changes in salinity at surveys 4 and 5, 7, and 8, and 30 and 31 (Fig. 2; Table 1).

Salinity decreased significantly from station 1 to station 5 (Fig. 3; Tables 2 and 3). Mean values changed from 19.2 ± 1.26 to 5.9 ± 1.06 ppt. Stations 2 and 3 were intermediate or transitional between stations 1, 4, and 5 (Table 3).

Salinity was significantly different with respect to depth strata (Table 2). The mean salinity increased from 10.6 ± 0.94 to 15.8 ± 1.07 ppt from surface to bottom, and surface values were significantly different from mid-water and bottom salinities.

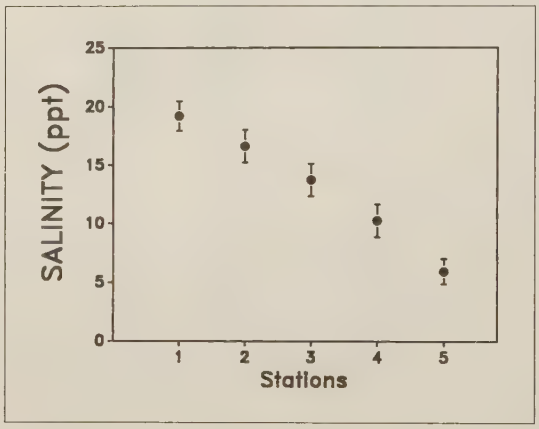

Figure 3
Distribution of mean salinity (ppt) over all surveys and depth levels along the 5 sampling stations. The vertical lines indicate ± 1 standard error.

Three vertical distribution patterns were observed for salinity: vertically homogeneous, with high or low salinity values in the entire water column; slightly stratified; and highly stratified (Fig. 2). Any one station, independent of its position in the estuary, could present any one of these patterns. Station 3, for example, was vertically homogeneous with low salinity during survey 32 (Summer/83) and with high salinity in survey 17 (Summer/82); it was slightly stratified during survey 13 (Spring/81); and it was highly stratified in survey 6 (Winter/81; Fig. 2).

Changes from one pattern to another could occur very rapidly, depending on the dominant meteorological con-

Table 2

Results of the three-way analysis of variance on temperature, salinity, and larval density. df = degrees of freedom; * = variances were significantly different ($P<0.05$); ** = variances were highly significantly different ($P<0.01$).

Source of variation		df	Dependent variables (Mean squares) Temperature	Salinity	Larval density
Within	Temperature	296	7.50		
	Salinity	340		1.36	
	Larval density	347			1.89
Season		3	259.75*	15.07*	43.49*
Station		4	5.23	7.68**	2.51
Depth		2	6.42	9.40**	1.11
Season by station		12	1.49	0.41	3.16
Season by depth		6	4.24	0.31	0.81
Station by depth		6	0.66	0.41	0.80
Season by station by depth		18	0.54	0.24	0.52

Table 3

Distance of the sampling stations from the ocean; temperature, salinity, and larval density at each station (Mean ± SE). ns = means are not significantly different between stations; a = mean salinities between stations 1, 2, and 3 are not significantly different; b = salinities between stations 2, 3, and 4 are not significantly different; c = mean salinities between stations 4 and 5 are not significantly different. (Multiple comparison test of Scheffé [$P<0.05$].)

Station	Distance from ocean (km)	Temperature (°C)	Salinity (ppt)	Larval density ($N/100m^3$)
1	3.7	19.6 ± 0.37(ns)	19.2 ± 1.26(a)	94.4 ± 12.92(ns)
2	17.6	20.1 ± 0.38(ns)	16.6 ± 1.40(ab)	68.5 ± 10.90(ns)
3	30.5	20.4 ± 0.42(ns)	13.7 ± 1.40(ab)	97.4 ± 18.00(ns)
4	44.4	20.2 ± 0.52(ns)	10.2 ± 1.40(bc)	66.7 ± 13.26(ns)
5	62.0	20.8 ± 0.53(ns)	5.9 ± 1.06(c)	83.4 ± 14.86(ns)

ditions. The large Patos Lagoon basin is drained exclusively through the narrow access channel. During winter and spring, high precipitation levels (Castello and Möller 1978) combined with moderate northerly winds (Costa et al. 1988) result in intense freshwater discharge. During these seasons, only sporadic strong southerly winds may intrude seawater into the channel area (Fig. 2). An increase in the estuarine salinity results from a decrease in freshwater run-off during summer and fall (Castello and Möller 1978) combined with either weak or moderate southerly winds (Costa et al. 1988), or with an increased tidal action on the estuary which is dampened during winter and spring by high freshwater run-off (Abreu 1987). However, the pattern of the salinity distribution depends on the interaction of all these forces. During survey 4 and 5, for example, the velocity of the southerly wind changed from approximately 36 to 4.5 km/h (Costa et al. 1988). This caused the mean salinity of the channel to decrease from 18.9 ± 3.0 to 2.2 ± 0.4 ppt (Table 1; Fig. 2).

Temperature also followed a seasonal pattern (Fig. 4). Mean values ranged from 24.3 ± 1.5 °C during spring to 13.7 ± 0.6 °C during winter (Table 1; Fig. 4). The horizontal distribution of temperature was relatively constant along the stations sampled (Fig. 5) and no significant differences were found among the station means (Table 2; Table 3). Temperature remained relatively constant over depth and no significant differences were found (Table 2). The fact that the estuary is shallow and well mixed prevents the development of thermal stratification.

Larval Abundance and Seasonal Distribution

Twenty families of fishes were represented in samples that included 27 taxa, 19 of which were identified to species

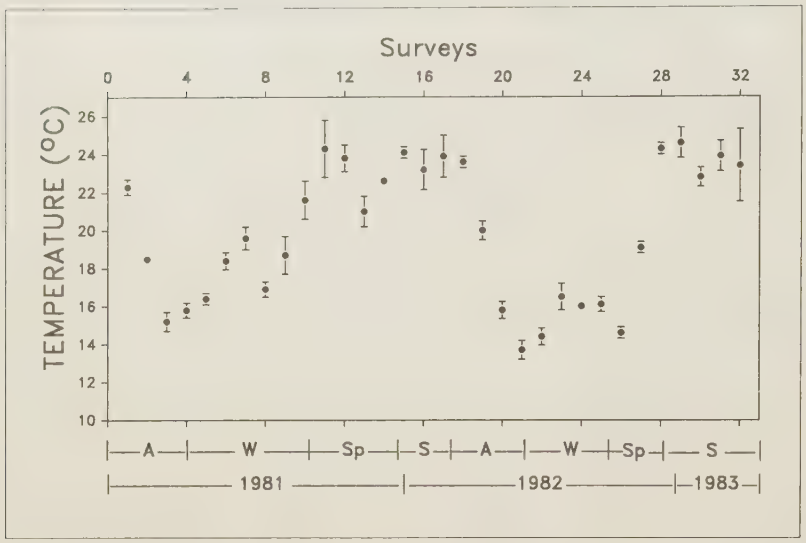

Figure 4
Distribution of mean temperature (°C) over all sample stations and depth levels for the 32 surveys. The vertical lines indicate ± 1 standard error. A = Autumn; W = Winter; Sp = Spring; S = Summer.

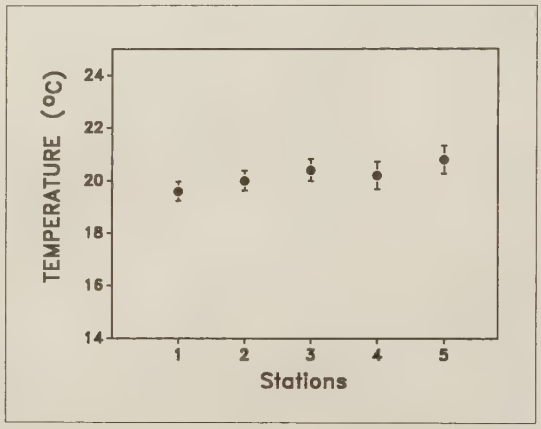

Figure 5
Distribution of mean temperature (°C) over all surveys and depth levels along the 5 sampling stations. The vertical lines indicate ± 1 standard error.

(Table 4). About 8.8% (primarily damaged clupeiform larvae) were unidentifiable. *Micropogonias furnieri*, *Brevoortia pectinata*, and *Lycengraulis* sp. were the most abundant species. Together they represented 65.4% of the total larval fish density, and their length distribution was between 1.8 and 12.0 mm SL, 2.9 and 21.0 mm SL, and 1.3 and 34.0 mm SL, respectively. The second group of taxa was less abundant and accounted for 23.4% of the total. These included *Parapimelodus valenciennis*; Blenniidae; *Trichiurus lepturus*; *Gobiesox strumosus*[1]; *Paralonchurus brasiliensis*; *Macrodon ancylodon*; *Paralichthys* sp.; Atherinidae; *Gobiosoma parri*; and *Menticirrhus* spp. A third group was composed of taxa whose relative abundance was less than 1% each and included *Achirus garmani*; *Syngnathus folletti*; *Gobionellus* spp.; *Peprilus paru*; *Cynoscion striatus*; *Umbrina canosai*; *Hyporhamphus kronei*; *Parona signata*; *Symphurus jenynsi*; *Anchoa marinii*; *Prionotus punctatus*; *Synagrops* sp.; *Mugil* spp.; and *Porichthys porosissimus*.

In general, the highest mean density of larvae was observed during the summer (Fig. 6; Table 1), during which time every species identified in the study, with the exception of *Prionotus punctatus* and *Porichthys porosissimus*, was present (Fig. 7). This was particularly evident during the summers of 1981 and 1982. Autumn showed the lowest mean larval density (Table 1). During this season *Brevoortia pectinata*, *Lycengraulis* sp., and Atherinidae were the dominant taxa, while *Anchoa marinii*, *Parapimelodus valenciennis*, *Hyporhamphus kronei*, *Syngnathus folletti*, *Mugil* spp., *Micropogonias furnieri*, *Paralonchurus brasiliensis*, and *Gobiosoma parri* were present, but not in large numbers (Fig. 7). During the period studied, winter and spring had a relatively higher density than autumn (Table 1). However, during winter, fewer species were present in the estuary (Fig. 7). An increase in the number of species and density was observed in spring, and the maximum density was reached in summer (Figs. 6 and 7).

The increase in larval fish density and composition, which occurred during spring and summer months, was associated with an increase in temperature (Figs. 4 and 7). Owing to its influence on spawning, temperature, rather than salinity, may influence the cycle of larval density (Flores-Coto et al. 1983; Houde and Alpern Lovdal 1984).

Two different patterns of seasonal distribution occurred in the Patos Lagoon estuary: one group of larvae occurred

[1] Johnson and Greenfield (1983) (Northeast Gulf Science 6(1):33-49) consider *Gobiesox barbatulus* rather than *G. strumosus* to be the form ocurring in Brazil. Based on the fact that there is only one species of *Gobiesox* in the Patos Lagoon, we decided to use *G. strumosus* following Chao et al. (1982b). Further investigation to determine which form is present in the southern coast of Brazil is necessary, but it is beyond the scope of this study.

Table 4

Absolute and relative mean density of fish larvae collected per cruise in the Patos Lagoon estuary. All stations and depth levels were combined.

Family	Species	Larval density [(*N*/100 m^3)/cruise]	Larval density (%)
CLUPEIDAE	*Brevoortia pectinata*	225.9	22.56
ENGRAULIDAE	*Anchoa marinii*	0.2	00.2
	Lycengraulis sp.	200.2	20.00
PIMELODIDAE	*Parapimelodus valencienis*	43.5	4.34
BATRACHOIDIDAE	*Porichthys porosissimus*	0.02	0.002
EXOCOETIDAE	*Hyporhampus kronei*	0.9	0.09
ATHERINIDAE	Atherinidae spp.	13.9	1.39
SYNGNATHIDAE	*Syngnathus folletti*	4.8	0.48
TRIGLIDAE	*Prionotus punctatus*	0.1	0.01
PERCICHTHYIDAE	*Synagrops* sp.	0.1	0.01
CARANGIDAE	*Parona signata*	0.6	0.06
SCIAENIDAE	*Cynoscion striatus*	2.3	0.23
	Macrodon ancylodon	18.4	1.84
	Menticirrhus spp.	11.0	1.10
	Micropogonias furnieri	229.2	22.89
	Paralonchurus brasiliensis	21.4	2.14
	Umbrina canosai	1.7	0.17
MUGILIDAE	*Mugil* spp.	0.1	0.01
BLENNIIDAE	Blenniidae spp.	36.1	3.61
GOBIIDAE	*Gobiosoma parri*	11.2	1.12
	Gobionellus spp.	3.3	0.33
TRICHIURIDAE	*Trichiurus lepturus*	34.3	3.43
STROMATEIDAE	*Peprilus paru*	2.6	0.26
GOBIESOCIDAE	*Gobiesox strumosus*	29.0	2.90
BOTHIDAE	*Paralichthys* sp.	14.9	1.49
SOLEIDAE	*Achirus garmani*	6.8	0.68
CYNOGLOSSIDAE	*Symphurus jenynsi*	0.2	0.02
Others		88.4	8.83

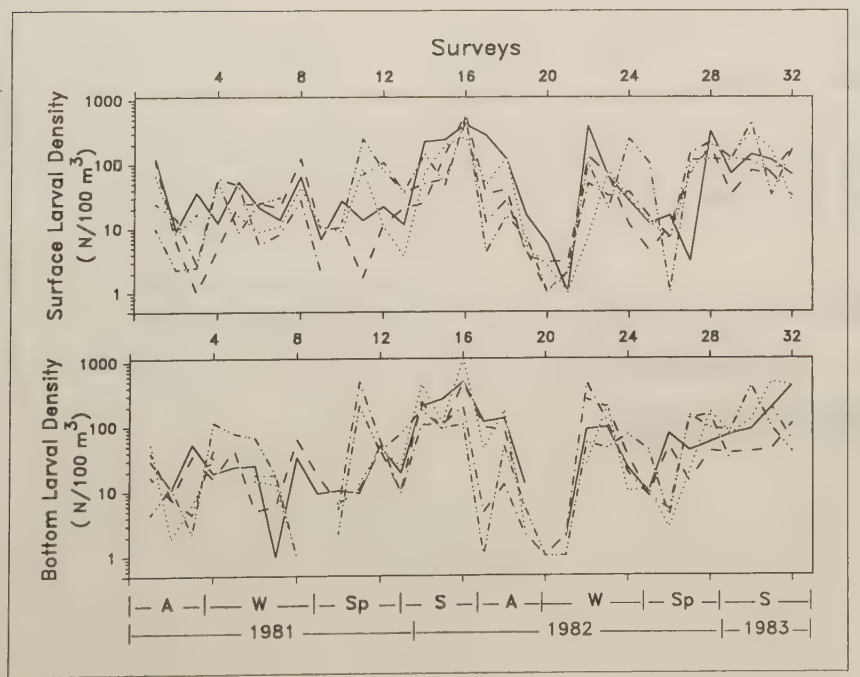

Figure 6

Distribution of larval density (*N*/100 m^3) at each station for the 32 surveys. (———) station 1; (- - -) station 2; (· · · · ·) station 3; (- · - · -) station 4; and (- · · - · · -) station 5. A = Autumn; W = Winter; Sp = Spring; S = Summer.

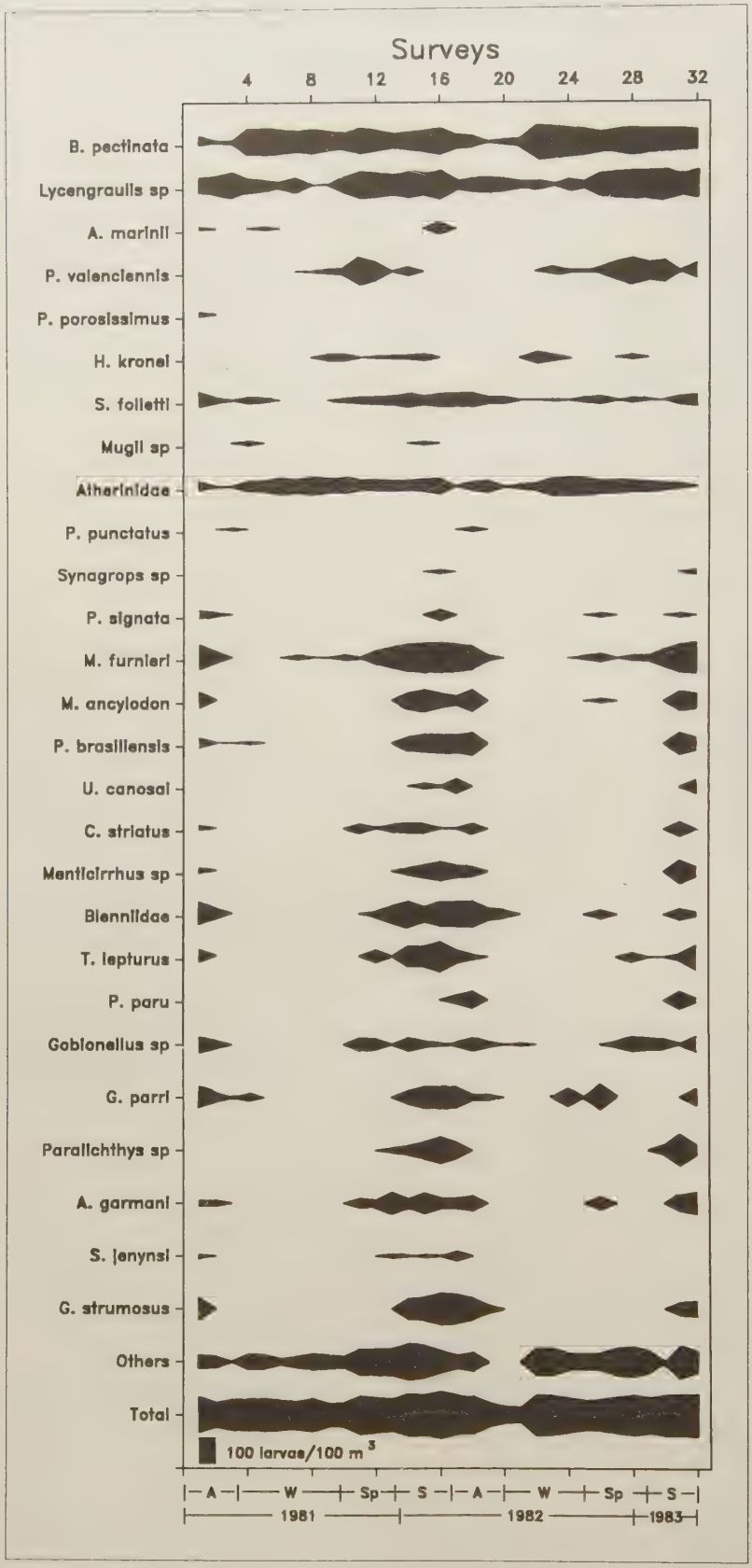

Figure 7
Distribution of total larval density ($N/100m^3$) expressed as $\ln(x + 1)$ for each identified species along the 32 surveys. A = Autumn; W = Winter; Sp = Spring; S = Summer.

continuously throughout the year, and another exhibited a discontinuous seasonal cycle (Fig. 7). *Brevoortia pectinata*, *Lycengraulis* sp., and Atherinidae represented the first group and their presence in the estuary suggested that these species reproduce during the entire year. The second group predominated during early spring and late summer and included *Micropogonias furnieri*, *Macrodon ancylodon*, *Paralonchurus brasiliensis*, Blenniidae, *Gobionellus* spp., *Peprilus paru*, *Trichiurus lepturus*, *Paralichthys* sp., and *Achirus garmani*.

Horizontal Distribution

Most of the species sampled showed a decrease in their density towards the interior of the estuary, whereas others, such as *Parapimelodus valenciennis*, increased. *Brevoortia pectinata*, *Lycengraulis* sp., Atherinidae, *Micropogonias furnieri*, and *Achirus garmani* were abundant throughout the entire estuary. *Hyporhamphus kronei* was most abundant in the central region of the estuary (stn. 3; Fig. 8).

The individual patterns of horizontal distribution and abundance reflected the origins of the species and the degree to which the estuary is used by them. Species with an oceanic origin, such as *Anchoa marinii*, *Porichthys porosissimus*, *Prionotus punctatus*, *Synagrops* sp., *Parona signata*, *Cynoscion striatus*, *Umbrina canosai*, *Mugil* spp., *Trichiurus lepturus*, *Peprilus paru*, and *Symphurus jenynsi*, occurred in the estuary during periods of strong salt water intrusion. This increase in salinity was the result of an increase in the frequency of southerly winds (Costa et al. 1988) which favor their transport into the estuary. They were generally restricted to regions influenced by the ocean (stns. 1 to 3), occurring only in low densities in the interior of the estuary (stns. 4 and 5; Fig. 8).

Species whose eggs and larvae originated in the adjacent coastal region were distributed along the entire estuary with a small decrease in abundance in the most interior waters. These species use the estuary as a nursery area for their larvae and juveniles, and include *Brevoortia pectinata*, *Lycengraulis* sp., *Macrodon ancylodon*, *Menticirrhus* spp., *Micropogonias furnieri*, and *Paralonchurus brasiliensis* (Fig. 8).

Atherinidae, *Syngnathus folletti*, Blenniidae, *Gobionellus* spp., and *Achirus garmani* are taxa that reside in the Patos Lagoon estuary and show a uniform density distribution throughout the entire channel (Fig. 8). However, the presence of more than one species in each of the above families could mask their individual distributional patterns.

Parapimelodus valenciennis is a freshwater species and showed a decrease in its density towards the ocean (Fig. 8). It is an uncommon species in the estuary and its presence is associated with periods of strong freshwater run-off. These larvae apparently cannot withstand increases in salinity, and they do not use the estuary as a nursery area.

Vertical Distribution

While most of the species showed a homogeneous vertical distribution, a few were selectively distributed with depth (Fig. 9). *Parapimelodus valenciennis*, *Umbrina canosai*, *Gobionellus* spp., *Trichiurus lepturus*, and *Achirus garmani* were most abundant at the bottom, whereas *Brevoortia pectinata*, *Lycengraulis* sp., *Parona signata*, *Gobiesox strumosus*, and *Symphurus jenynsi* showed highest densities at the surface. *Anchoa marinii* was found at the surface and bottom, *Porichthys porosissimus* was present only at the bottom, and *Mugil* spp. occurred at surface and mid-water levels.

The vertical distribution of fish larvae in estuaries is generally related to tidal flow (Graham 1972; Weinstein et al. 1980; Fortier and Leggett 1982). In the Patos Lagoon estuary, astronomic tides have a very small amplitude and their flow can be amplified or reduced by the action of either wind (Costa et al. 1988) or precipitation in the drainage basin (Castello and Möller 1978). Consequently, the vertical distribution of fish larvae probably does not reflect a well-defined circulation pattern.

Different groups of larvae presented different patterns of vertical distribution (Fig. 9). Weiss (1981) found this selective distribution to be related to the salinity structure of the water column. According to her, *Brevoortia pectinata*, *Lycengraulis* sp., *Parapimelodus valenciennis*, and Atherinidae are abundant in less saline surface waters, while *Micropogonias furnieris* and *Trichiurus lepturus* are frequently found near the more saline bottom waters. In this study, however, *Parapimelodus valenciennis* and Atherinidae did not exhibit this pattern. *Parapimelodus valenciennis* was found to be more abundant at the bottom than near the surface (Fig. 9). This may have been the result of a large number of larvae being captured during an anomalous period of freshwater run-off in the spring of 1982 (Fig. 2). At this time, this species dominated the entire estuary (Fig. 7). The abundance of Atherinidae was high at the surface and at the bottom with a decrease in mid-water levels (Fig. 9). Three atherinid species occur in the Patos Lagoon estuary (Chao et al. 1982b) and their individual distributions could be associated with different depths.

Conclusion

Micropogonias furnieri, *Brevoortia pectinata*, and *Lycengraulis* sp. are the most abundant fish larvae in the channel area of the Patos Lagoon estuary. Fish larvae are present throughout the year in the estuary, and abundance and diversity increases during the months of spring and summer, with an increase in temperature. The larvae are distributed along the entire estuary and in the entire water column. This general picture of seasonal, horizontal, and vertical distribution can be altered by the meteorological conditions prevailing in the estuary. Further studies should be con-

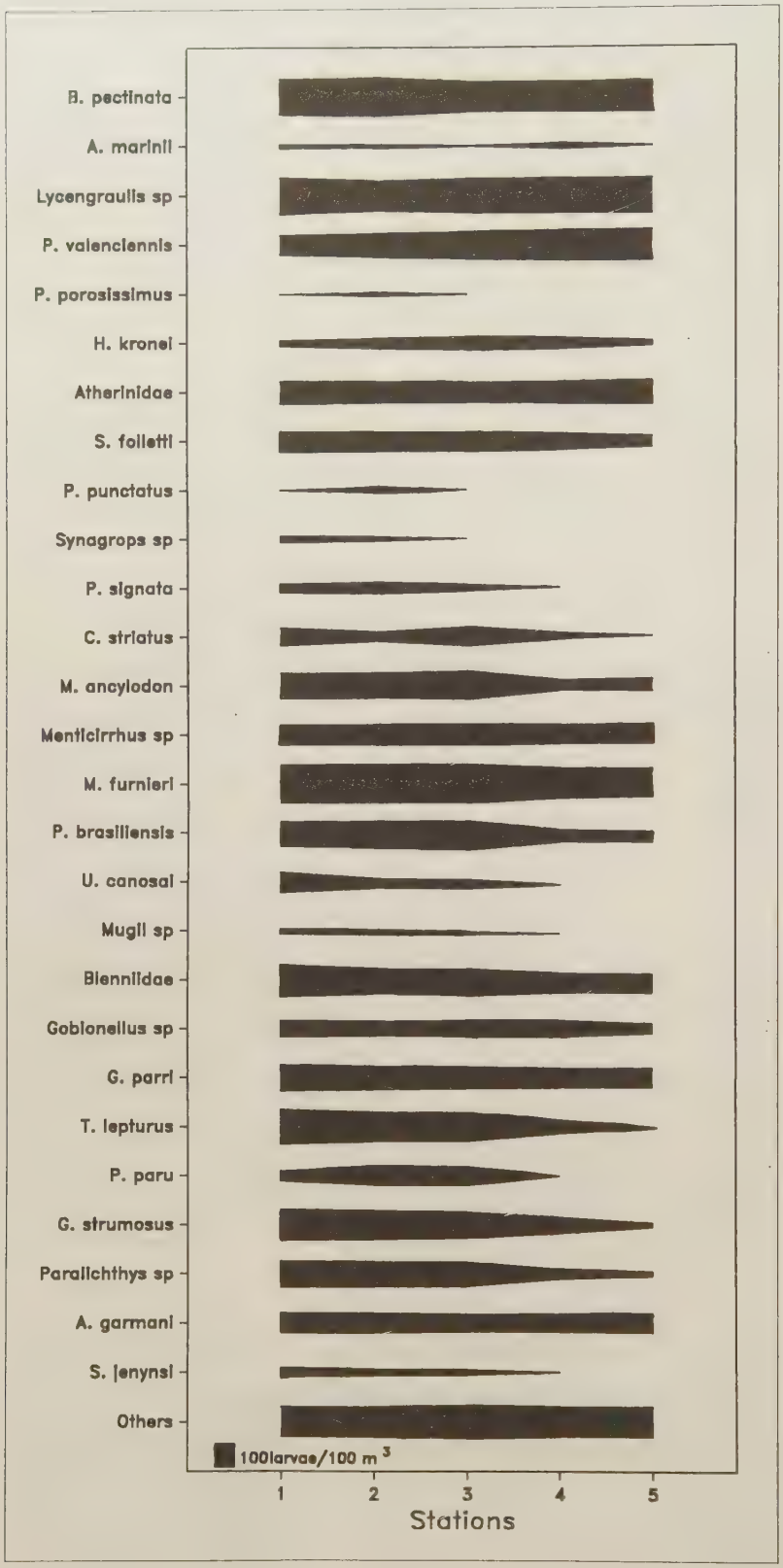

Figure 8
Distribution of total larval density ($N/100m^3$) expressed as $\ln(x + 1)$ for each identified species at the 5 sampling stations.

ducted to understand specific distribution patterns better. These studies should take into account the biology and ecology of individual species and the dynamic character of the Patos Lagoon estuary.

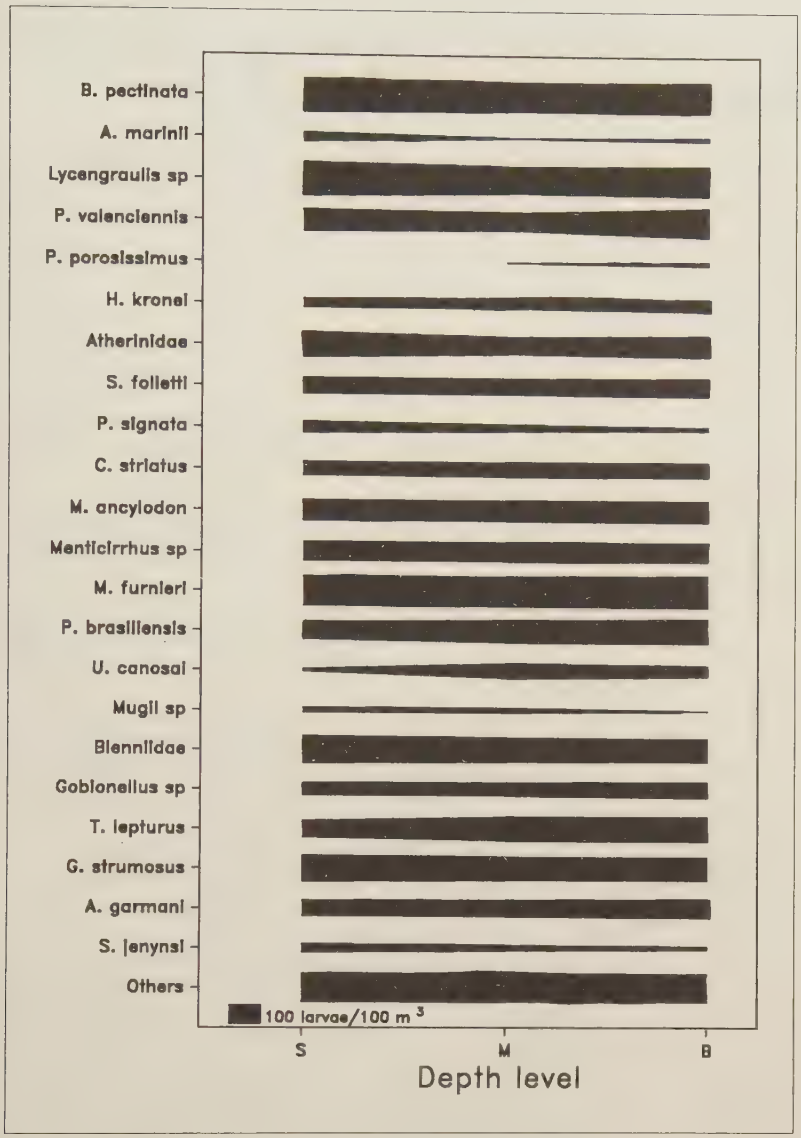

Figure 9
Distribution of total larval density ($N/100m^3$) expressed as $\ln(x + 1)$ for each identified species at the 3 depth levels. S = surface waters; M = mid-water; B = bottom-waters.

Acknowledgments

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Larval Distribution and Abundance of Myctophidae, Gonostomatidae, and Sternoptychidae from the Southern Gulf of Mexico

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ABSTRACT

Larval distribution and abundance of Myctophidae, Gonostomatidae, and Sternoptychidae from the southern Gulf of Mexico were studied. The material was collected during four cruises from 1983 to 1984. The family Myctophidae with 2618 larvae, was represented by 12 genera and at least 19 species; Gonostomatidae, with 1101 larvae, by 10 genera and at least 13 species; and Sternoptychidae, with 146 larvae, by two genera. *Diaphus* spp. (47.5 individuals/m^2 sea surface [= L]), *Cyclothone* spp. (27.6/L), *Benthosema suborbitale* (29.1/L) and *Maurolicus muelleri* (23.3/L) were the most abundant taxa. The highest frequency of occurrence and greatest abundance of larvae were recorded over the slope and at oceanic stations, which likely corresponded to the principal spawning areas. Only the most abundant taxa occurred frequently over the outer shelf, and occasionally in shallow areas (<50 m). Only 10 out of the 28 species showed evidence of seasonality, presenting their highest larval abundance only during some of the cruises; *Hygophum hygomii*, *Centrobranchus nigroocellatus*, *Vinciguerria poweriae* and *Pollichthys mauli* were most abundant in winter, *Myctophum asperum* in spring, *Bonapartia pedaliota* in summer, *Hygophum reinhardtii* and *Maurolicus muelleri* in spring and summer, and *Notoscopelus resplendens* and *Myctophum selenops* in the winter and spring.

Introduction

The ichthyoplanktonic composition of mesopelagic fishes is not well known on a worldwide scale (Hopkins and Lancraft 1984; Roe and Badcock 1984), the southern Gulf of Mexico being among the least studied regions. An investigation of larvae of the families Gonostomatidae, Sternoptychidae, and Myctophidae in the southern Gulf of Mexico was undertaken in the present study as part of the research program of the Laboratorio de Zooplancton, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. These families were chosen because of their high relative abundance in the area.

Larval stages of the species in these families are only partially known, owing in part to their great specific diversity, as about 60 genera and more than 330 species are represented (Ahlstrom et al. 1984; Moser et al. 1984).

For the southern Gulf of Mexico and Caribbean Sea, 16 genera and 43 species of Myctophidae, 15 genera and 19 species of Gonostomatidae, and 3 genera and 8 species of Sternoptychidae have been recorded (Rass 1971; Naf-paktitis 1975; Shiganova 1977; Houde et al. 1979; Fahay 1983; Richards 1984; Romero and del Castillo 1984; Gartner et al. 1987). Studies directed at the larval stages in these families in the southern Gulf and Caribbean Sea have been scarce. The most extensive has been that by Houde et al. (1979) who recorded 16 genera and 25 species from the northeast part of the Gulf. There have been no specific investigations into our study area, except for one which Flores-Coto et al. 1988 composed a species list.

The main objectives of the our study were to contribute to the knowledge of the composition, distribution, and abundance of the species comprised by these families and to define their spawning seasons and areas.

Study Area

The study area included the southwestern portion of the Gulf of Mexico, limited to the north by lat. 21° N and comprising the continental shelves of Veracruz, Tabasco, and Campeche, and adjacent oceanic zones. The slope is delineated as the 182 m isobath (Fig. 1).

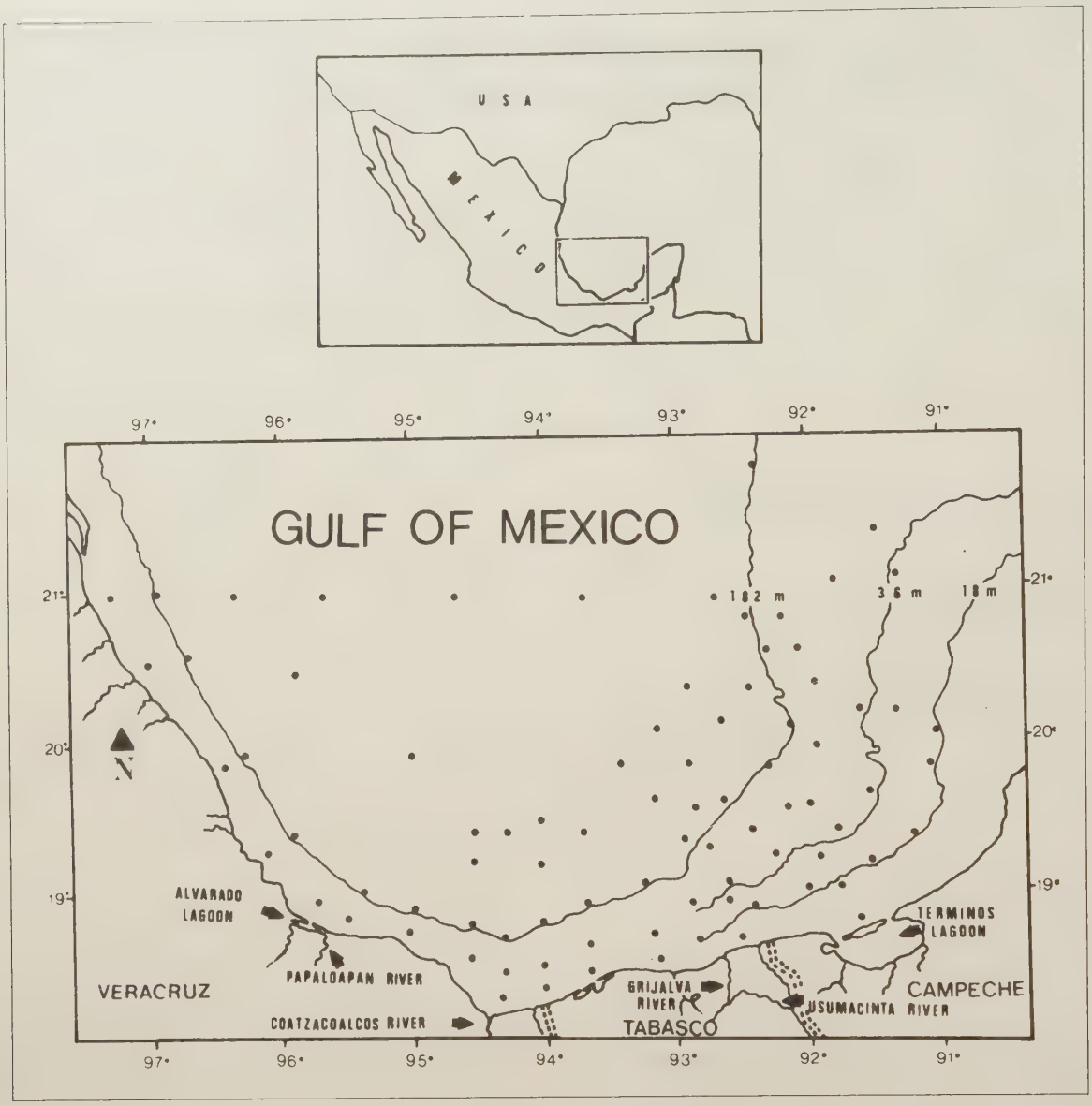


Figure 1
Study area and location of stations during the cruises. Subsequent figures are for sampling stations of specific cruises.

Material and Methods

Zooplankton samples were collected aboard the oceanographic ship *Justo Sierra*, during four cruises: PROGMEX I (31 March–8 April 1983, "spring"); IMECO (15–25 February 1984, "winter"); PROGMEX II (25 April–4 May 1984, "spring"); and PROGMEX III (7–17 August 1984, "summer").

A sampling pattern was established mainly over the continental shelf, covering a larger portion of the oceanic zone during the IMECO cruise (Fig. 1). Zooplankton sampling consisted of a double-oblique plankton tow following a circular course using a 60-cm bongo net with 333- and 505-micron mesh nets. The water volume filtered was calculated using flowmeters placed in each net. The depth and tow time varied from 18 to 200 min and 5 to 23 min, respectively, according to bathymetry. Ship speed was held between 1.5 and 2 kn. Each sample was fixed in 4% formalin buffered with sodium borate.

Fish larvae were sorted from each sample and myctophids, gonostomatids, and sternoptychids separated for study. Larval density was standardized as number of larvae per 10 m^2 of sea surface ("L") (Houde et al. 1979; Richards 1984),

$$L_j = \frac{C_j Z_j}{V_j} \times 10,$$

Table 1

Abundance of Myctophidae larvae. Number of positive stations (S), number of larvae (N), and mean larval density (L) (per 10 m^2 of sea surface) are given for each cruise.

	PROGMEX-I 49 stations			IMECO 29 stations			PROGMEX-II 40 stations			PROGMEX-III 55 stations			Mean	
Taxa	S	N	L	S	N	L	S	N	L	S	N	L	No.	%
Diaphus spp.	29	326	52.59	18	142	41.13	24	233	57.70	34	222	38.43	47.46	18.35
Benthosema suborbitale	18	86	29.51	16	105	36.23	20	74	20.83	26	119	29.80	29.09	11.25
Notolychnus valdiviae	13	36	15.69	10	31	17.50	12	37	19.99	22	95	26.28	19.86	7.68
Lampanyctus spp.	10	25	11.86	14	85	35.64	7	11	9.22	13	19	10.27	16.75	6.48
Hygophum taaningi	19	45	11.81	7	11	8.21	11	22	10.47	12	20	10.61	10.27	3.97
Diogenichthys atlanticus	10	14	8.90	7	10	8.05	14	31	12.31	22	40	10.80	10.01	3.87
Hygophum macrochir	3	7	12.00	8	14	10.03	4	4	5.58	1	2	12.04	9.91	3.83
Myctophum nitidulum-affine	17	34	10.53	11	17	8.42	14	25	11.78	18	22	8.35	9.77	3.78
Hygophum reinhardtii	14	25	8.76	8	9	6.69	10	14	8.19	22	39	12.01	8.91	3.45
Myctophum asperum	2	3	8.44	3	3	5.88	6	10	13.70	3	3	5.83	8.46	3.27
Myctophum obtusirostre	3	6	6.85	3	6	12.50	3	3	3.10	5	7	9.47	7.98	3.09
Centrobranchus nigroocellatus	3	3	5.21	3	7	12.82	3	4	8.14	1	1	4.47	7.66	2.96
Hygophum hygomii	1	1	2.69	9	24	15.79	3	4	4.96	1	1	6.27	7.43	2.87
Notoscopelus resplendens	7	11	9.18	11	22	10.73	3	3	7.15	0	0	0.00	6.76	2.62
Myctophum selenops	9	15	9.17	4	5	6.62	8	14	9.96	0	0	0.00	6.44	2.49
Myctophum spp.	9	16	10.33	0	0	0.00	10	12	6.43	8	11	7.30	6.01	2.33
Lepidophanes spp.	5	13	9.23	0	0	0.00	5	6	9.02	2	2	4.49	5.68	2.20
Hygophum sp.	1	2	7.94	0	0	0.00	0	0	0.00	1	2	6.42	3.59	1.39
Lobianchia gemellarii	0	0	0.00	1	1	7.31	0	0	0.00	0	0	0.00	1.83	0.71
Ceratoscopelus warmingii	0	0	0.00	1	1	5.39	0	0	0.00	0	0	0.00	1.35	0.52
Hygophum benoiti	0	0	0.00	0	0	0.00	2	2	3.16	0	0	0.00	0.79	0.31
Myctoph-indeter.	10	102	44.51	17	189	61.10	10	29	15.65	15	23	9.07	32.58	12.60
Total		770	275.18		682	310.02		538	237.32		628	211.90	258.60	100

where L_j = number of larvae at station j under 10 m^2 of sea surface
C_j = the catch of larvae at station j
Z_j = the depth (in meters) at station j
V_j = the volume filtered by the net (in cubic meters) at station j

As two samples were available for each station, resulting from the 333- and 505-micron nets, the highest value of larval density was always taken for each taxon, independently of the mesh. This treatment was based on the assumption that some taxa may be more efficiently sampled by either the 505- or 333-micron mesh.

Results

A total of 3863 larvae were identified. Of those, 2618 corresponded to myctophids with 12 genera and at least 19 species; 1101 gonostomatids with 10 genera and at least 13 species, and 146 sternotychids, represented by 2 genera and at least 2 species (Tables 1 and 2).

Species identifications in the genera *Diaphus*, *Lampanyctus*, *Lepidophanes*, *Cyclothone*, *Sternoptyx*, *Argyropelecus*, and in some specimens of *Myctophum* and *Hygophum* were difficult and will, therefore, be treated at the generic level. The larvae of *Myctophum nitidulum* and *Myctophum affine* could not be distinguished from each other and will be treated as the complex "*M. nitidulum-affine.*" Species are considered by family and are listed in decreasing order of generic abundance.

Family Myctophidae

Diaphus spp. (47.5/L), *Benthosema suborbitale* (29.1/L), *Notolychnus valdiviae* (19.0 L), and *Lampanyctus* spp. (161.7/L) were the most abundant taxa, accounting for about 43.7% of all myctophids collected (Table 1). Larvae of these taxa occurred during all four oceanic cruises, where they were widely distributed, and caught at virtually all oceanic and slope stations (Figs. 2, 3, 4, and 5). *Lampanyctus* spp. occurred at a somewhat lower frequency than the other taxa, and its larvae were scarce over the continental shelf, generally occurring at stations greater than 100 m in depth (Fig. 5). *Hygophum* was the next most abundant taxon, accounting for about 15.8% of the family, although no one species was especially common (maximum 10.3 L). *Hygophum* species had a wide distribution at the slope and

Table 2

Abundance of Gonostomatidae and Sternoptychidae larvae. Number of positive stations (S), number of larvae (N), mean larval density (L) (per 10 m^2 of sea surface) are given for each cruise.

	PROGMEX-I (spring) 49 stations			IMECO (winter) 29 stations			PROGMEX-II (spring) 40 stations			PROGMEX-III (summer) 55 stations			Mean	
Taxa	S	N	L	S	N	L	S	N	L	S	N	L	No.	%
Cyclothone spp.	22	102	22.32	17	100	32.87	23	150	37.06	28	87	18.20	27.62	19.65
Maurolicus muelleri	9	46	36.36	4	8	9.38	14	47	17.98	25	121	29.61	23.33	16.60
Vinciguerria poweriae	10	17	9.06	4	27	36.41	10	24	13.80	14	24	10.30	17.39	12.38
Pollichthys mauli	8	16	10.66	7	28	17.95	4	4	6.84	0	0	0.00	8.86	6.30
Gonostoma atlanticum	6	11	8.99	6	8	6.82	8	10	7.28	15	20	7.84	7.73	5.50
Vinciguerria attenuata	4	4	6.39	9	11	6.78	8	14	10.53	11	13	6.78	7.62	5.42
Vinciguerria nimbaria	7	9	5.58	6	8	7.71	7	11	8.68	6	6	7.68	7.41	5.28
Gonostoma elongatum	1	1	11.23	8	11	8.05	0	0	0.00	12	14	7.51	6.70	4.77
Bonapartia pedaliota	0	0	0.00	1	1	4.65	1	1	6.30	4	7	12.34	5.82	4.14
Ichthyococcus ovatus	0	0	0.00	0	0	0.00	1	1	5.34	2	2	6.67	3.00	2.14
Margrethia obtusirostra	0	0	0.00	1	1	6.02	0	0	0.00	3	3	5.53	2.89	2.05
Valenciennellus tripunctulatus	0	0	0.00	2	2	4.86	1	1	6.39	0	0	0.00	2.81	2.00
Diplophos taenia	1	1	2.58	0	0	0.00	0	0	0.00	0	0	0.00	0.65	0.46
Gonost-indeter.	10	34	22.58	12	32	16.75	9	27	19.21	12	36	16.33	18.72	13.32
Total-Gonostomatidae		241	135.76		237	158.25		290	139.41		333	128.77	140.55	100
Sternoptyx sp.	3	5	13.40	14	55	21.36	11	25	15.36	19	42	14.31	16.11	72.80
Argyropelecus spp.	2	2	7.37	0	0	0.00	6	7	7.68	6	10	9.03	6.02	27.20
Total-Sternoptychidae		7	20.77		55	21.36		32	23.04		52	23.34	22.13	100

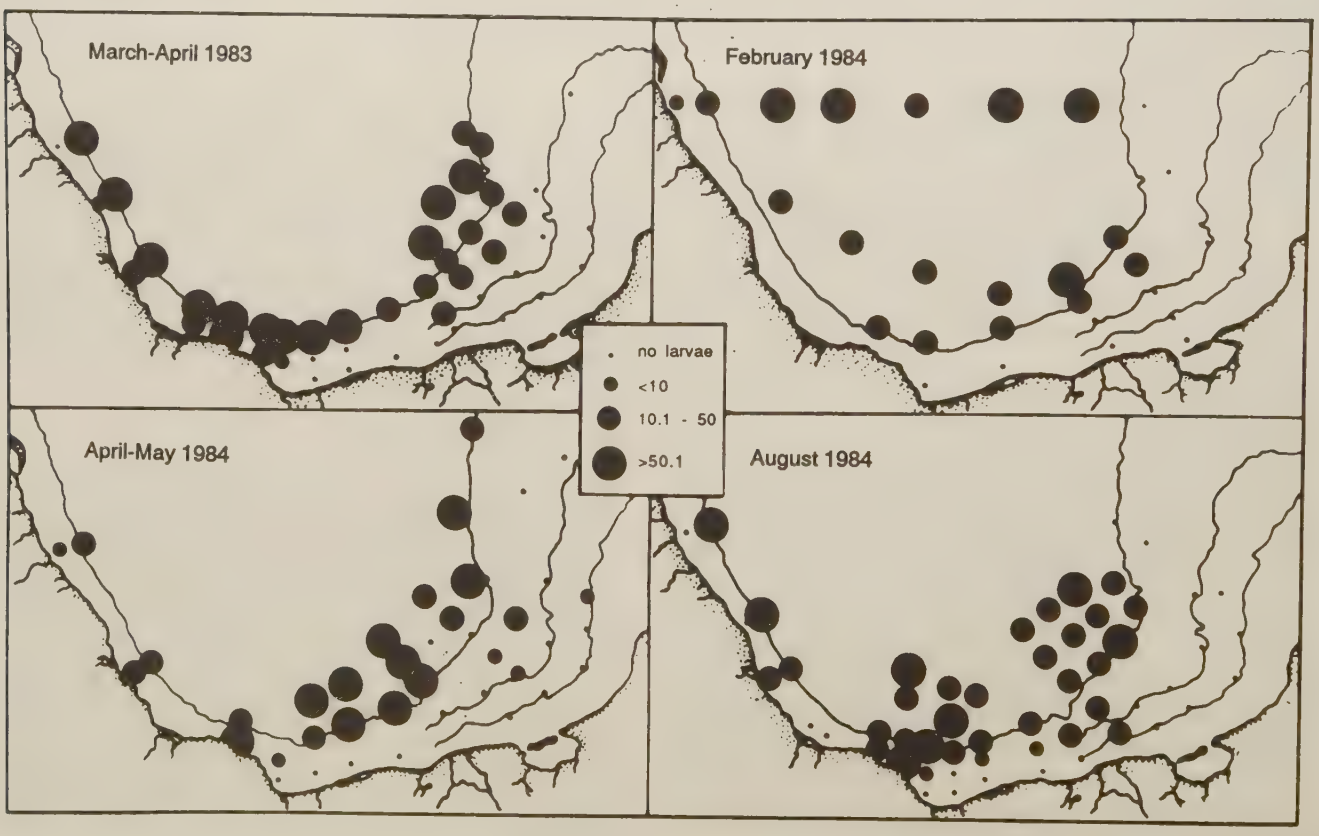
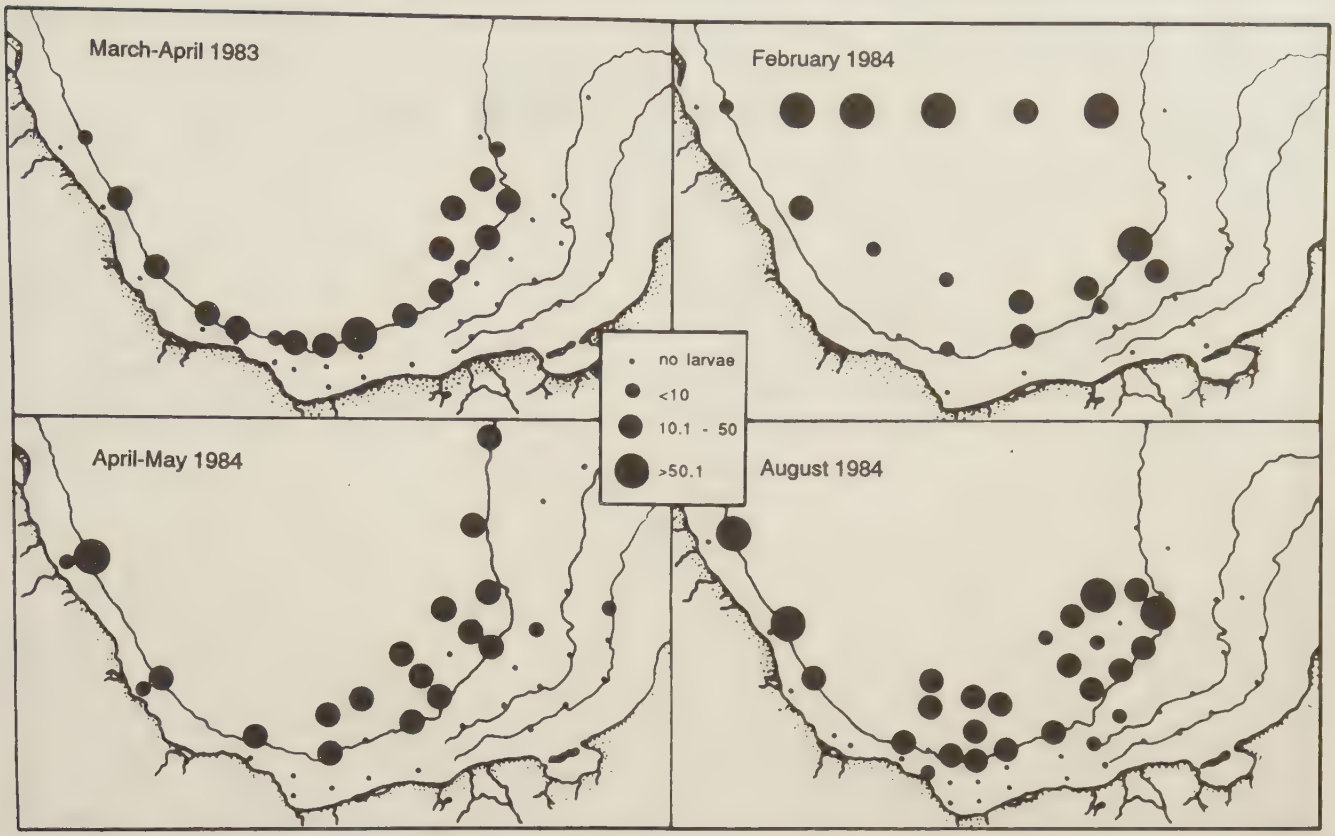


Figure 2

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Diaphus* spp., southern Gulf of Mexico. Smallest dots represent stations with no larvae.



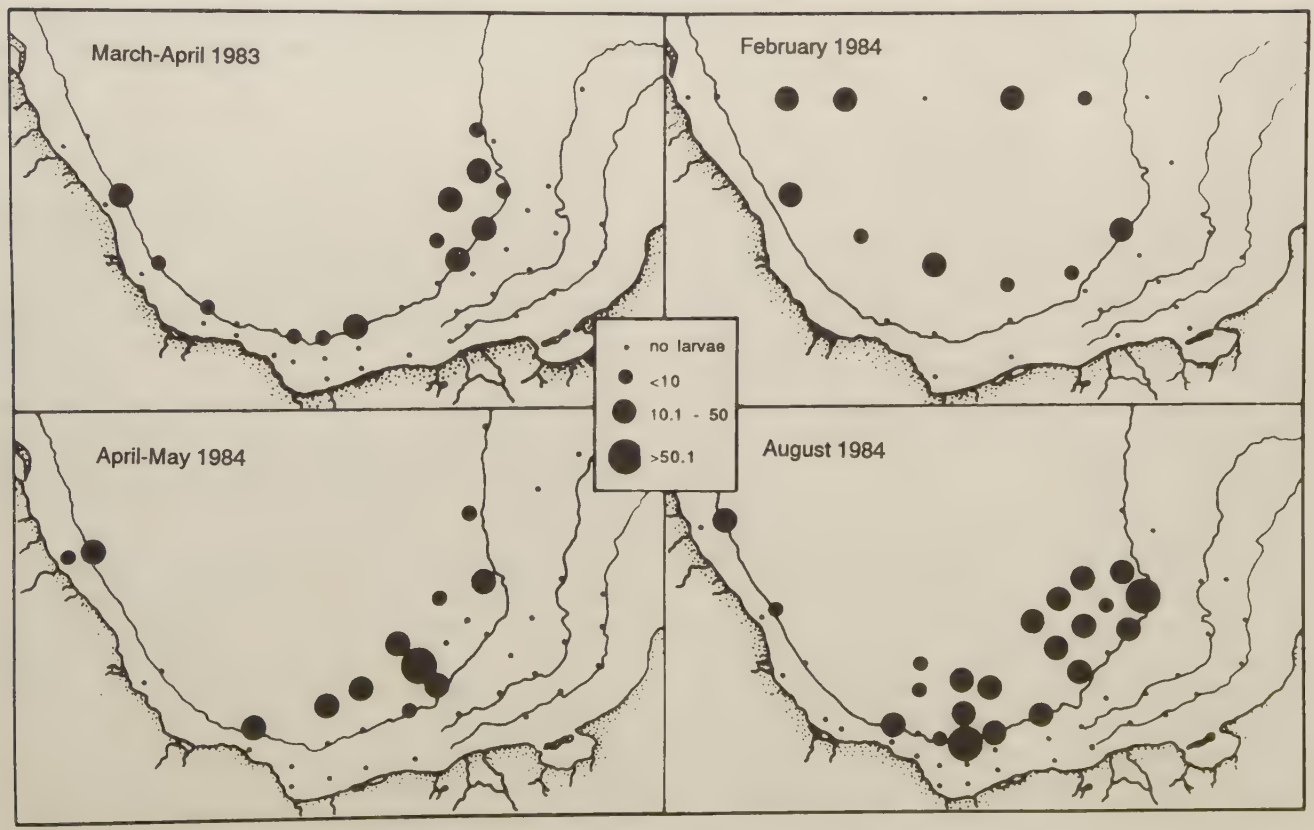


Figure 3 (top)

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Benthosema suborbitale*, southern Gulf of Mexico. Smallest dots represent stations with no larvae.

Figure 4 (bottom)

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Notolychnus valdiviae*, southern Gulf of Mexico. Smallest dots represent stations with no larvae.

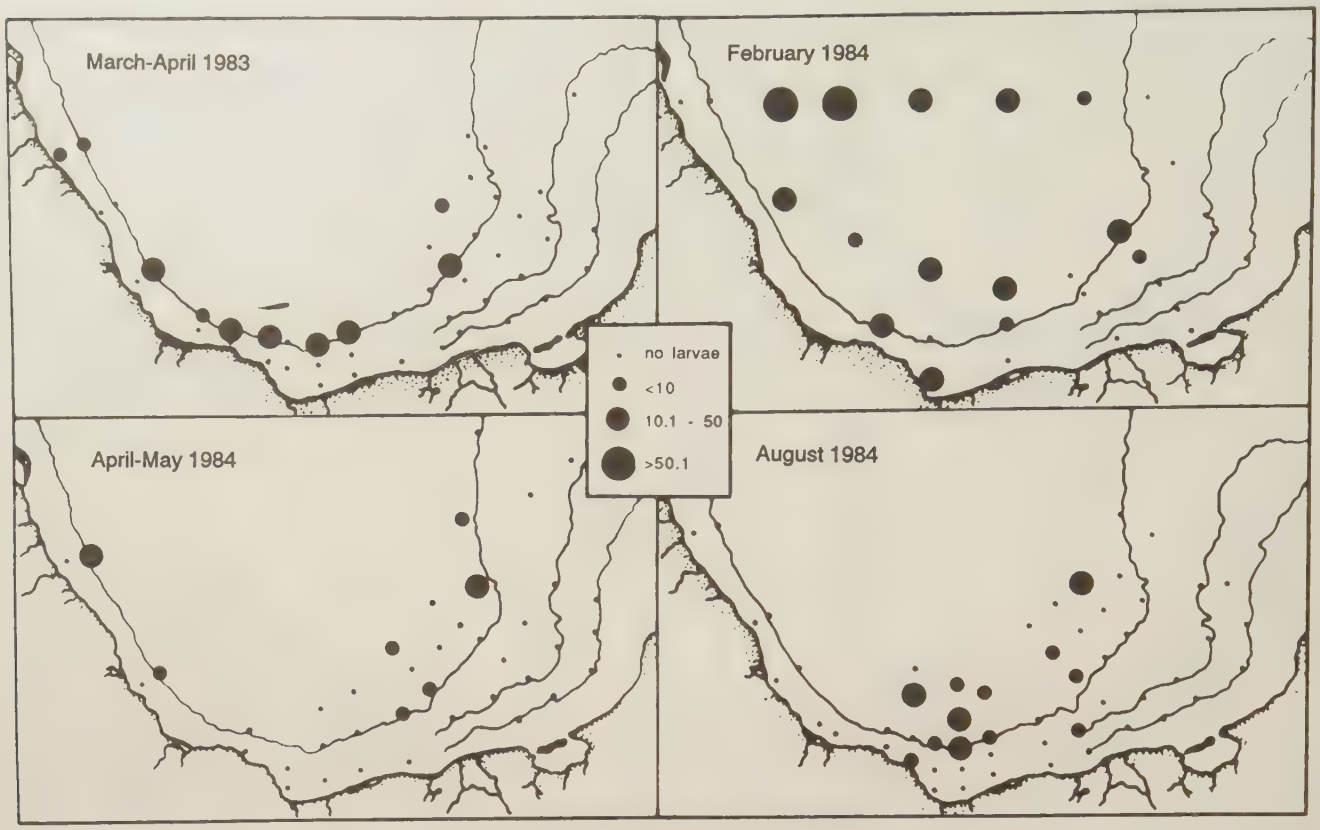


Figure 5

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Lampanyctus* spp., southern Gulf of Mexico. Smallest dots represent stations with no larvae.

oceanic zones, but were only occasionally found over the continental shelf. *Hygophum taaningi* and *H. reinhardtii* had relatively high frequencies of occurrence.

The genus *Myctophum* represented 14.9% of the family, although, as for *Hygophum*, the individual species were not very abundant (maximum 9.8 L). All species had a low frequency of occurrence except for *M. nitidulum-affine*. The larvae of *Myctophum* had a wide distribution and were principally caught at oceanic and slope stations; over the continental shelf they were scarce and larvae of *M. asperum* were not recorded in this area.

Diogenichthys atlanticus represented 3.9 % of the family (7.7/L), and was sixth in frequency of occurrence. All larvae were captured at slope and oceanic stations, except for three stations over the continental shelf.

The remaining myctophid taxa, *Centrobranchus nigroocellatus*, *Notoscopelus resplendens*, *Lobianchia gemellarii*, and *Ceratoscopelus warmingii*, were scarce. These species were recorded at oceanic stations and over the continental slope. Six myctophid species appeared to show seasonal peaks of abundance (Table 1). They included *Hygophum hygomii* and *Centrobranchus nigrocellatus* (winter peak); *Hygophum reinhardtii* (spring/summer peak); *Myctophum asperum* (spring peak); and *Notoscopelus resplendens* and *Myctophum selenops* (winter–spring peak).

Family Gonostomatidae

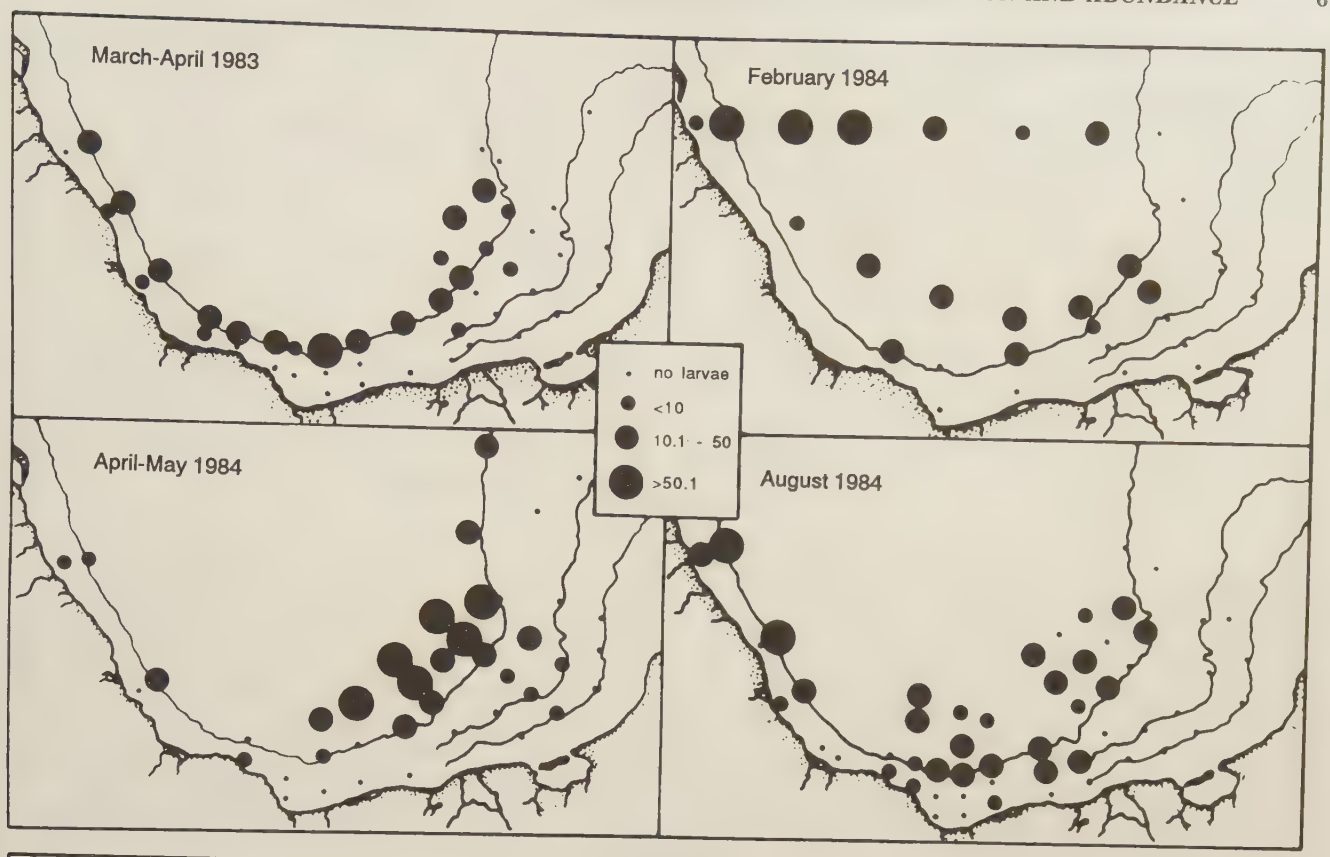
Of the gonostomatids, *Cyclothone* spp. (27.6/L), *Maurolicus muelleri* (23.3/L), *Vinciguerria poweriae* (17.4/L), *Vinciguerria attenuata* (7.6/L), *Vinciguerria nimbaria* (7.4/L), *Pollichthys mauli* (8.9/L), *Gonostoma atlanticum* (7.7/L), and *Gonostoma elongatum* (6.7/L) were most frequent and had the highest mean densities.

Cyclothone spp. were widely distributed in the oceanic zone and over the continental slope, where they were caught at almost all stations sampled; over the shelf they were present less frequently but were found at some stations less than 50 m depth (Fig. 6).

Maurolicus muelleri and the three *Vinciguerria* species were distributed widely along the slope and oceanic zones; they were occasionally recorded over the shelf (Figs. 7 and 8).

Larvae of *G. atlanticum* and *G. elongatum* were not captured over the continental shelf, but they were broadly distributed in the slope and oceanic areas, although *G. elongatum* was only found at one station during the spring cruises. *Pollichthys mauli* larvae were mostly restricted to stations over the continental slope and the nearby oceanic areas, being found only once over the shelf.

The remaining gonostomatids, *Bonapartia pedaliota*, *Margrethia obtusirostra*, *Valenciennellus tripunctulatus*, *Ichthyococcus*



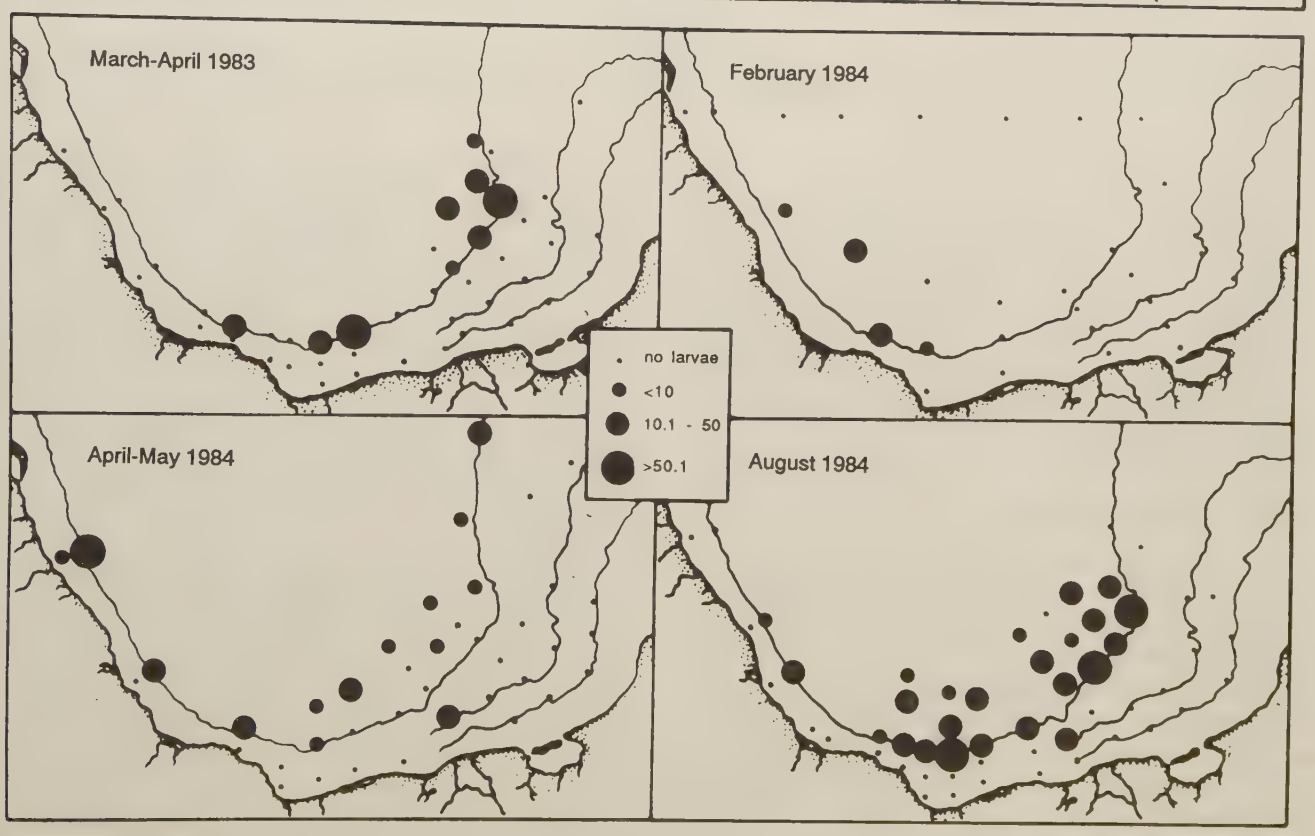


Figure 6 (top)

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Cyclothone* spp., southern Gulf of Mexico. Smallest dots represent stations with no larvae.

Figure 7 (bottom)

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Maurolicus muelleri*, southern Gulf of Mexico. Smallest dots represent stations with no larvae.

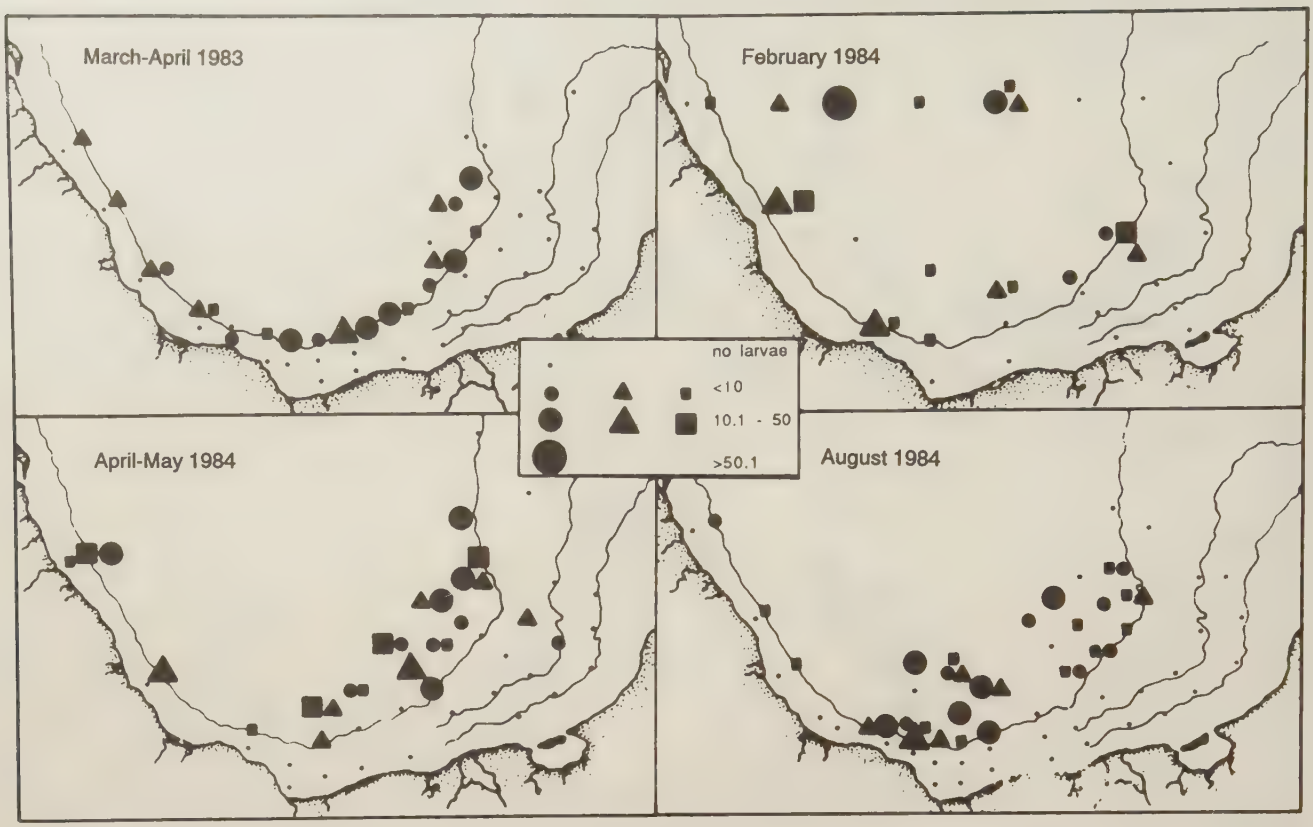


Figure 8

Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Vinciguerria poweriae* (●), *Vinciguerria attenuata* (■) and *Vinciguerria nimbaria* (▲), southern Gulf of Mexico. Smallest dots represent stations with no larvae.

ovatus, and *Diplophos taenia*, were scarce or rare. With the exception of *D. taenia*, which was collected over the shelf, these species were present only in samples from oceanic and slope stations. Seasonal peaks of abundance were apparent for 4 gonostomatid species (Table 2). They included *Vinciguerria poweriae* and *Pollichthys mauli* (winter peak), *Maurolicus muelleri* (spring/summer peak), and *Bonapartia pedaliota* (summer peak).

Family Sternoptychidae

Sternoptyx sp. was the most abundant and frequent taxon of this family, with a mean density of 16.0 L (Fig. 9). Larvae of *Argyropelecus* spp. were scarce and were not caught during the February cruise.

The higher abundance and frequency of occurrence of both taxa were recorded in the oceanic area; they were scarce over the shelf. Highest densities of *Sternoptyx* sp. were recorded in winter; however, this taxon was common year-round.

Discussion and Conclusions

The relative abundance and composition of taxa found in this study closely corresponded to data collected from the northeast Gulf of Mexico (Houde et al. 1979) and the Caribbean Sea (Richards 1984).

In the present study, the family Myctophidae had the highest number of larvae and taxa. *Diaphus* spp., *B. suborbitale*, *N. valdiviae*, and *Lampanyctus* spp. accounted for more than 43% of the myctophids, whereas *Cyclothone* spp., *M. muelleri*, and *V. poweriae* were most abundant among the gonostomatids, accounting for about 40% of this family, and *Sternoptyx* sp. made up approximately 70% of the sternoptychids.

The relative abundances of these taxa closely resembled the records of Houde et al. (1979) for the northeast Gulf, where *Diaphus* spp. were the most abundant taxa; the relative abundances of the remaining taxa differed only slightly. Species differing in relative abundance between the southern and northeastern Gulf of Mexico included *Maurolicus muelleri* (second in abundance among gonostomatids in the present study but the most abundant gonostomatid in the northeast Gulf) and *Gonostoma atlanticum* (common in the our study but rare in the northeast Gulf).

Differences between the southern Gulf and the Caribbean Sea (Richards 1984) were large in terms of relative

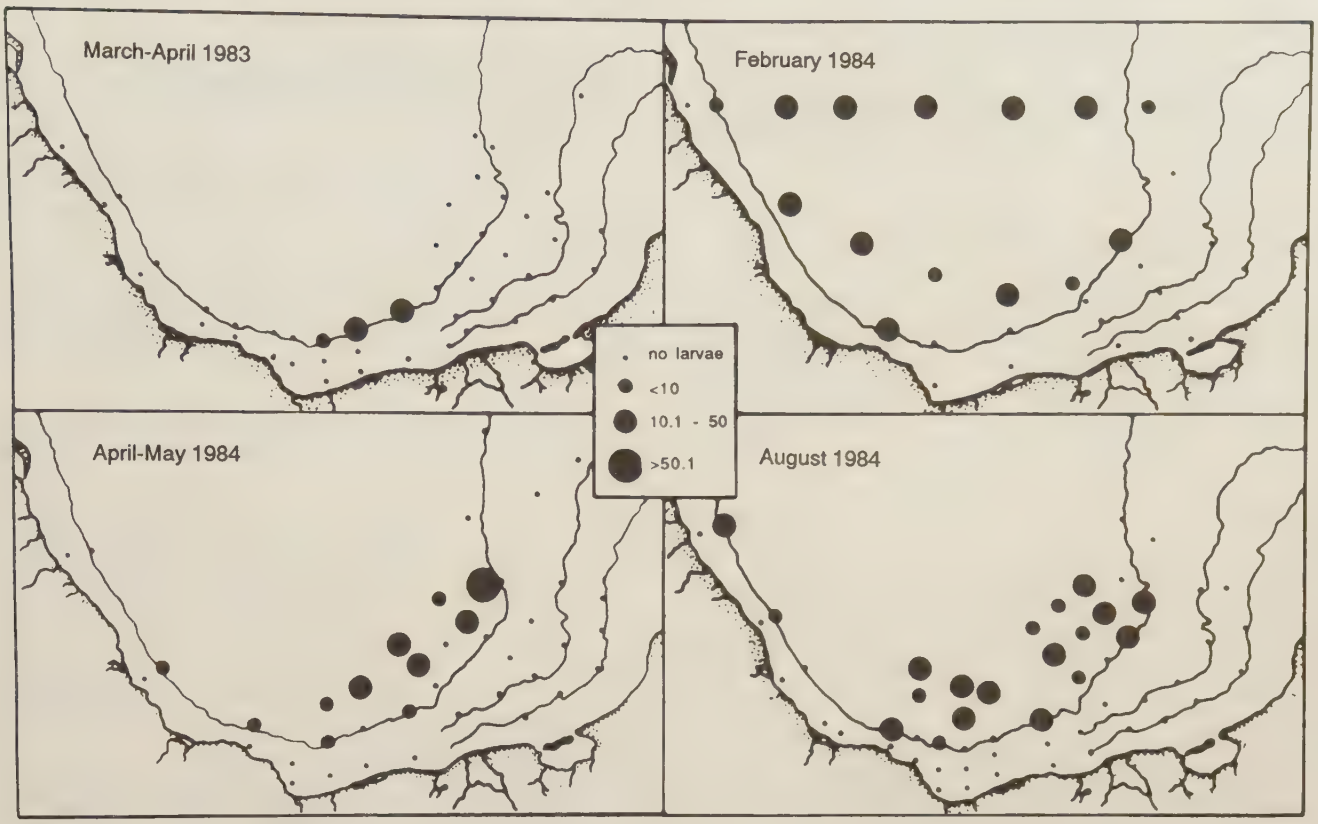


Figure 9
Abundance (number of larvae per 10 m^2 of sea surface) and distribution of *Sternoptyx* sp., southern Gulf of Mexico.

abundances of taxa; however, species compositions were very similar. In contrast to our findings, Richards (1984) reported *C. warmingii*, *P. mauli*, and *G. elongatum* to be abundant; whereas *B. suborbitale*, *D. atlanticus*, *M. muelleri* and *V. poweriae* were found to be rare. These differences may have been related to sampling periodicity, however, since the Caribbean area was sampled only during winter and summer.

The distribution patterns of all species collected in this study can be considered to be primarily oceanic. However, many species, particularly the most common ones, had at least some larvae in the neritic zone, principally at the outer zone of the wide shelf of Tabasco–Campeche or over the narrow shelf of Veracruz, where mixing of neritic and oceanic water takes place. Some of these species were occasionally captured in areas less than 50 m depth. The distribution of scarce or rare species, such as *M. asperum*, *L. gemellarii*, *C. warmingii*, *B. pedaliota*, *V. tripunctulatus*, *M. obtusirostra*, *I. ovatus*, and *Argyropelecus* spp., was restricted to the oceanic area.

The wide distribution of species in the oceanic area suggests that spawning usually takes place in deep zones and that migration of larvae to neritic waters occurs by means of currents. Thus similar distributions should be expected over geographically distant shelves such as those of Florida and Tabasco–Campeche. However, the narrowness of the Florida shelf allows most of the species in these families to occur at depths less than 100 m.

Only 10 out of the 28 recorded species showed evidence of seasonality, presenting their highest abundances only during some of the cruises. *Hygophum hygomii*, *Centrobranchus nigroocellatus*, *Vinciquerria poweriae* and *Pollichthys mauli* were most abundant in winter, *Myctophum asperum* in spring, *Bonapartia pedaliota* in summer, and *Hygophum reinhardtii* and *Maurolicus muelleri* in the period of spring and summer; whereas the greatest abundance of *Notoscopelus resplendens* and *Myctophum selenops* larvae were recorded in the winter and spring.

The seasonal patterns of these species do not correspond with the data for these northeast Gulf (Houde et al. 1979) or for the Caribbean (Richards 1984), except for *M. muelleri* which was principally recorded in summer in the northeast Gulf, and during spring and summer in this study.

Most of the species which exhibited seasonal abundance peaks in the northeast Gulf and Caribbean were most abundant in the summer. In our study area, *B. pedaliota* was the only species which had its highest occurrence in this period, but this species was rare in the other study areas.

Identification and comparison of seasonal trends in this and other studies may have been limited by the low

numbers of cruises made (four in this study and two in the Caribbean). However, differing environmental conditions between the study areas should also be considered as a potential factor for influencing the spawning periods of these species.

Acknowledgments

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Larval Migration and Mortality Rates of Bay Anchovy in the Patuxent River

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ABSTRACT

The distribution, migration patterns, and mortality of bay anchovy (*Anchoa mitchilli*) were studied in the Patuxent River subestuary of Chesapeake Bay from 1 June to 17 August 1987. The size-specific distribution of larvae indicated hydrodynamic transport from downriver spawning areas to upriver nursery areas. This distribution was evidenced by many small larvae and few large larvae downriver opposed to relatively more large larvae and few small larvae upriver. An alternative hypothesis, that this pattern was caused solely by differential mortality between upriver and downriver portions of the estuary, was eliminated. Mortality rates were computed with a decreasing rate function of length from the Pareto family using abundance data that are censored for a range of growth rates found in the literature (3 mm/wk and 4 mm/wk). Mortality rate estimates varied from 0.161 to 0.162 per mm of growth at 10 mm total length (TL) and from 0.064 to 0.079 per mm of growth at 20 mm TL. The mortality rate function derived here is compared to a range of constant mortality rates estimated for larval bay anchovies in Biscayne Bay, Florida. Mortality rates for the Pareto model were greater than the constant estimates for larvae less than two days old and became less than the constant mortality rates for larvae greater than five days old. As a result the net mortalities estimated by the Pareto model for the Patuxent River were much less by the time larvae were eight days old.

Introduction

This study is a component of an entrainment impact assessment for the Chalk Point Electric Generating Station on the Patuxent River, a tributary of the Chesapeake Bay Estuary. The assessment determines the geographic boundaries of the larval bay anchovy, *Anchoa mitchilli*, population in the Patuxent River and estimates recruitment. Geographic boundaries of the population are determined by analysis of the migration patterns of the larvae. Recruitment is estimated through standing crop estimates and a mortality function. An independent assessment has been done for Maryland's Power Plant Research Program (Polgar et al. 1988) and is the subject of ongoing studies. Here, we present the findings relative to the migration of larval bay anchovy in the Patuxent River and an improved methodology for estimating larval mortality rates.

The bay anchovy is a suitable subject for the study of fisheries dynamics because it is abundant over a wide geographical area and it is accessible to sampling. Eggs are free floating; small larvae are initially planktonic; and larger larvae, juveniles and adults, are pelagic. Bay anchovy range from the Gulf of Maine to the Yucatan Peninsula (Hildebrand 1963), is one of the dominant species in the Chesapeake Bay area (Hildebrand and Schroeder 1928), and is an important forage species (Hollis 1952; Merriner 1975; Chao and Musick 1977). Bay anchovy populations appear to be regulated largely by events occurring during the first few months of life (Vouglitois et al. 1987).

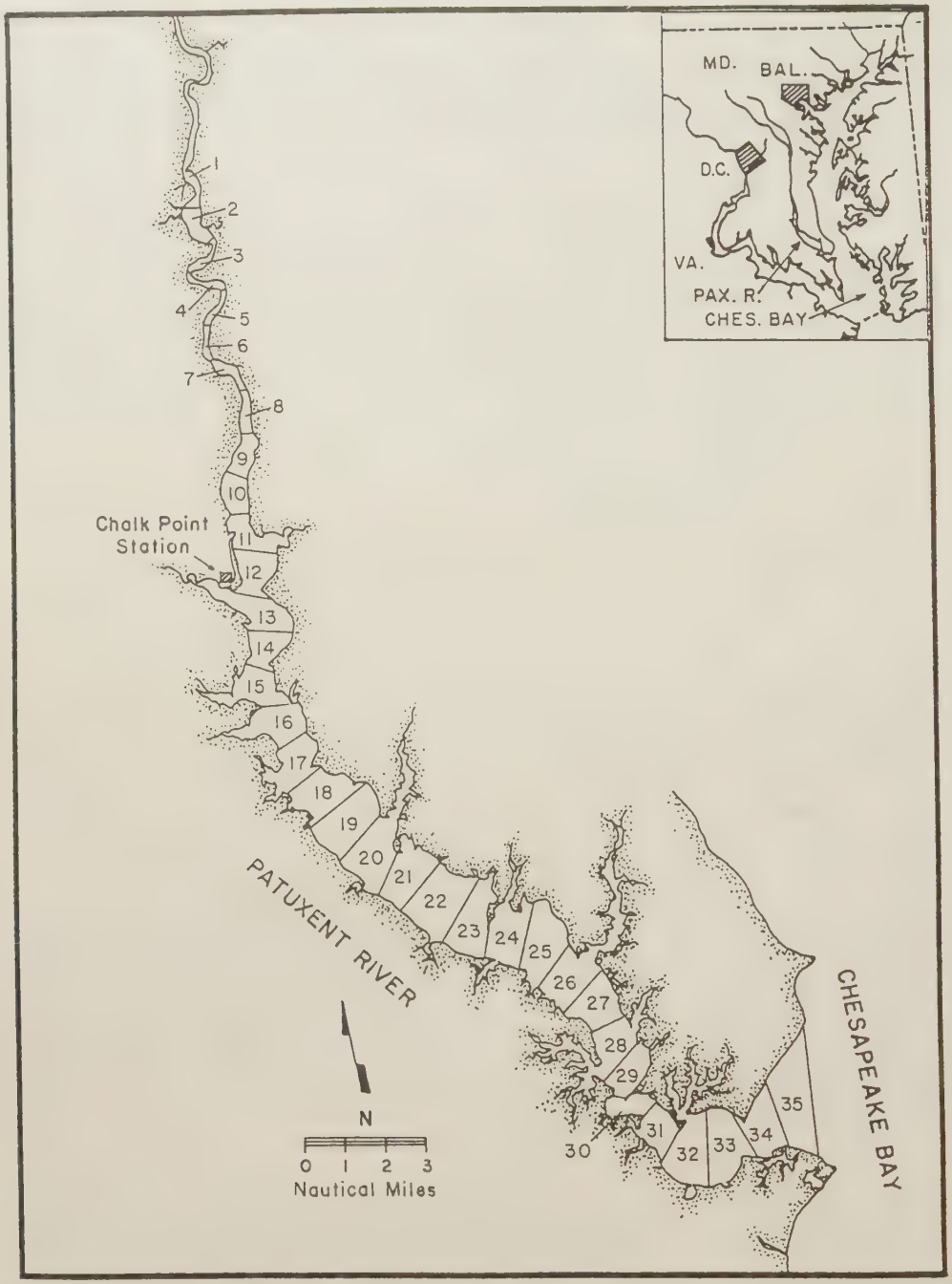

Figure 1
Map of the Patuxent River estuary with segment boundaries used to refer to sampling locations in this study. Segment boundaries are nautical river miles of Cronin and Pritchard (1975). The following abbreviations are used in the inset: BAL = Baltimore, MD; D.C. = Washington, District of Columbia; CHES BAY = Chesapeake Bay; PAX R. = Patuxent River.

Bay anchovy spawning in the Chesapeake Bay extends from the Atlantic Ocean (Olney 1983) nearly to freshwater at the upper end of tributary rivers (Dovel 1971). The extent of spawning upriver is thought to be controlled by salinity. The bay anchovy can spawn in waters with salinity as low as 1 part per thousand (ppt), but they typically do not spawn in waters less than 6 ppt (Dovel 1971). Maximum spawning occurs in waters of 13 to 15 ppt. This study was designed to sample the region of the Patuxent that begins above and extends below the area of maximum spawning activity.

Bay anchovy spawning in the upper Chesapeake Bay and Patuxent River occurs from April to September with a peak in July (Dovel 1971). Spawning occurs at night (Ferraro 1980a, 1980b) and the eggs require approximately 20 to 24 hours to hatch (J. Cowan, Chesapeake Biological Laboratory, Solomons, MD. pers. commun. Nov. 1989; Kuntz 1914) and produce larvae approximately 2 to 3 mm total length (TL) (Wang and Kernehan 1979).

The Patuxent River is located in Maryland, USA. Its confluence with Chesapeake Bay is on the West side in the middle portion of the bay above that of the Potomac River

Table 1
Methods employed in three sampling programs.

	Sampling Program		
	Regional study	Diel study	Egg study
Patuxent River segments	4 to 35	35 and 10 to 14	4 to 35
Chesapeake Bay	One transect	Not sampled	Not sampled
Sampling dates (1987)	1 June to 19 August[a]	15 June to 17 August	29 June to 19 August
Frequency	Weekly	Biweekly	Weekly
Diel periods included	Night	Day and night	Day
Sampling gear	0.25-m^2 Tucker Trawl	1.0-m^2 Tucker Trawl	0.25-m Tucker Trawl
Type of tow	Discrete depth	Discrete depth	Stepped oblique
Sampling design	Random stratified	Random stratitified	Fixed station

[a]Transect across Chesapeake Bay at mouth of Patuxent River sampled from 29 June to 17 August.

(Fig. 1). The Patuxent River Estuary is 61 km long and has a volume of 695 million m^3 and a surface area of 113 km^2 (Edinger et al. 1989).

Freshwater inflow to the Patuxent River Estuary during the summer spawning season averages 5 m^3/sec. Most of the estuary is mesohaline (Academy of Natural Sciences, Philadelphia (ANSP) 1983). During this period, the lower deep portion of the estuary (maximum depth, 29 m) is partially mixed with a gradual longitudinal salinity gradient (Edinger et al. 1989). Near river segment 14 (Fig. 1) the estuary becomes shallow (maximum depth, 4 m), has a steep longitudinal salinity gradient. Depth increases in segment 11 (maximum depth, 6 m), and the water column remains partially mixed.

This paper gives results of studies of various aspects of bay anchovy recruitment. First, a description of sampling methods is presented, followed by a description of analytical methods for assessing temporal and spatial distribution. A mortality model based on the assumption that mortality rate is an inverse function of larval length is introduced. This is followed by results and discussion to assess the merits of the decreasing mortality rate model relative to a constant mortality rate model and to evaluate the hypothesis that bay anchovy larvae originate in the lower section of the Patuxent River estuary and migrate to the middle section of the estuary.

Sampling Methods

Bay anchovies in the Patuxent River estuary reportedly spawn near the river mouth and move to nursery areas upriver (Dovel 1971). Vertical and longitudinal distributions of eggs and larvae during this study verified this migration phenomenon. Distribution of eggs and larvae were observed in three sampling programs (Table 1). The geographic location of samples was determined with reference to 35 river segments (Fig. 1). There was no sampling above segment 4. Earlier studies (Setzler et al. 1979) indicated few bay anchovy larvae above segment 4.

The regional study specified that collections be made over a 12-week period from 1 June to 19 August 1987. The 35 segments were grouped into 9 regions, each with up to 4 depth layers (Fig. 1, Table 2), resulting in a total of 32 sampling cells. From 29 June to 19 August collections were made at four depths at randomly selected locations along a transect across the Chesapeake Bay at the mouth of the Patuxent River. During each week two nighttime collections were made from each of the Patuxent river cells and at each depth along the Chesapeake Bay transect. These collections were made with a 0.25-m^2 Tucker trawl with 253-μ mesh. A General Oceanics model 2030R flow meter was mounted in the mouth of the net to quantify volume filtered. Tows were of 2-min duration and the mean sample volume was 25 m^3. Salinity was measured at the surface and bottom in each segment.

The diel study specified day and night sampling and employed a larger net. A 1.0-m^2 Tucker trawl with 253-μ mesh was used to sample each of three depth layers in segment 35 at the mouth of the river and in segments 10 to 14 upriver. Three depth layers were sampled at each location and 6 to 9 samples were collected in each depth layer. Sampling was done every two weeks at alternate locations during the period 15 June to 17 August. These tows were also of 2-min duration and the mean sample volume in both areas was about 100 m^3.

Densities of eggs and newly hatched larvae were monitored by sampling weekly during the day for the period 29 June to 3 August. Samples were collected from five to six fixed locations within each of three river sections: lower river (segments 26 to 35), middle river (segments 14 to 25), and upper river (segments 4 to 13). Oblique tows of variable duration were taken and the mean sample volume was 65 m^3. Sampling was done between 0900 and 1500

Table 2

Hypsographic data for sampling regions in the Patuxent River Estuary (From Cronin and Pritchard 1975 and Edinger et al. 1989).

Region (segments included)[a]	Length (m × 10)	Surface area (m^2 × 10)	Volume (m^3 × 10)	Mean depth (m)	Sampling depth layers[b]
1 to 3	5.56	1.95	4.8	2.46	1,2,3
4 to 7	7.41	1.67	8.3	4.97	1,2,3
8 to 11	7.41	5.50	13.6	2.47	1,2,3
12 to 13	3.70	5.59	15.1	2.70	1,2,3
14 to 17	7.41	12.74	42.4	3.33	1,2,3,4
18 to 21	7.41	19.04	96.6	5.07	1,2,3,4
22 to 25	7.41	20.82	122.2	5.87	1,2,3,4
26 to 29	7.41	15.43	136.7	8.87	1,2,3,4
30 to 33	7.41	15.28	155.2	10.16	1,2,3,4
34 to 35	3.70	14.74	99.6	6.76	1,2,3,4

[a]Each segment is 1.85 km (1 nautical mile) in length. There was no sampling above segment 4. Earlier studies (Setzler et al. 1979) indicated few bay anchovy larvae above segment 4.

[b]Layer 1 represents depth from 0 to 1 m; layer 2, 1 to 3 m; layer 3, 3 to 8 m; Layer 4, 8m to bottom. Layers 3 and 4 were pooled in analysis.

hours. Sampling during the day allowed some mixing to occur between the spawning event the night before and sampling, and reduced the patchiness of the egg distribution resulting in less variance.

Larvae 4- to 23-mm TL were considered to be sampled effectively. Larvae less than 4-mm TL were subject to loss owing to extrusion (Houde and Lovdal 1984) through the sampling net and to poor sorting efficiency during sample processing. Thus only larvae greater than 3-mm TL were used in mortality computations. Larvae greater than 7-mm TL exhibited gear avoidance and appropriate corrections were implemented before making standing crop estimates.

Analytical Methods

Distribution and Migration

Analysis of variance (ANOVA) followed by a Tukey multiple range test was used to evaluate longitudinal and vertical differences in densities of eggs and larvae grouped in 4-mm length categories. Densities were transformed by the logarithmic expression

$$z = \log_e\left(\frac{n}{V} + 1\right); \quad (1)$$

where z = response variable analyzed
n = count of larvae in the sample
V = volume sampled by the gear.

In this transformation, densities were standardized to the mean sample volume, thus retaining the approximate lognormal distribution of the counts. A graphical check (Tukey 1962; Draper and Smith 1981) found that normality assumptions and homogeneous variance assumptions were met when data were standardized by this transformation.

Size distributions of larvae collected at the mouth of the river (segment 35) during the diel study were compared graphically with those collected in the upper portion of the river (segments 10 to 14).

Standing crop estimates were based on data from 0.25-m^2 Tucker trawl collections. Adjustments in densities obtained with the 0.25-m^2 Tucker trawl were made to reflect size specific sampling efficiency. This correction was derived by comparison of densities of larvae collected with the 0.25-m^2 trawl with those obtained with a 1.0 m^2 trawl. Larvae less than 7 mm TL apparently did not avoid the smaller net. This correction factor, estimated by least squares for larvae greater than 7 mm, was based on the following expression:

For $L > 7$:

$$\log_e(D_{1.0}) - \log_e(D_{0.25}) = -0.2656 + 0.0418\,L; \quad (2)$$

where
$\log_e(D_{0.25})$ = logarithm transform as shown above for larval density in 0.25 m^2 Tucker trawl (density units—number per 100 m^3);
$\log_e(D_{0.1})$ = logarithm transform as shown above for larval density in 1.0 m^2 Tucker trawl; (density units—number per 100 m^3);
L = total length (mm).

Table 3
Selected growth rates of the bay anchovy reported in the literature.

Growth rate (mm/d)	Type of study	State	Source
0.43 to 0.55	laboratory	FL	Saksena and Houde 1972
0.48	field	NC	Fives et al. 1986
0.43 to 0.56	field	FL	Leak and Houde 1987
0.39 to 0.62	mesocosm	MD	Cowan and Houde (1989)[a]
0.58 to 0.62	field	NY	Castro and Cowen (in press)

[a] Preliminary publication cited with permission of the authors.

The correction factor was obtained by exponentiating the difference:

$$\frac{D_{1.0}}{D_{0.25}} = e^{(-0.2656 + 0.0418\,L)}, \text{ for } L > 7;$$

$$\frac{D_{1.0}}{D_{0.25}} = 1, \qquad \text{for } L \leq 7. \tag{3}$$

Standing crops were estimated by multiplying the adjusted density of larvae in each cell by the volume of each of the 32 sampling cells. Cell volumes were estimated from the geometry of the estuary (Cronin and Pritchard 1975). The total standing crop is reported by river section.

Mortality

The larval mortality model assumed that the mortality rate was inversely proportional to length scaled by a power transformation, i.e.,

$$\frac{d\,N_L}{d\,L} = \frac{-\alpha\,N_L}{L^{\beta}}; \tag{4}$$

where L = length;
N_L = the number of larvae of length L;
α, β = model parameters, $\alpha > 0$, $\beta \geq 0$.

This differential equation integrates to the following survival model:

$$\log_e (N_L) = \frac{-\alpha}{1-\beta} L^{(1-\beta)} + c; \tag{5}$$

where c = a constant of integration.

This model is a member of the Pareto family of survival models (Miller 1981; Arnold 1985). For nonlinear least squares estimation new parameters were assigned to yield the following equation:

$$\log_e (N_L) = \alpha' L^{\beta'} + c; \tag{6}$$

where $\alpha' = -\alpha/(1-\beta)$;
$\beta' = (1-\beta)$.

The mortality rate per individual was obtained by dividing both sides of the initial differential equation by N_L and by changing the sign to express the fractional decrease in N_L as positive. Thus the mortality rate per individual is $\alpha L^{-\beta}$.

The assumptions required to apply this model are 1) there can be no immigration or emigration of larvae from the system; 2) length must be a valid proxy for age; and 3) sampling is sufficiently frequent to sample all cohorts within the spawning season. If the mortality model is applied to individual cohorts within the spawning season, an additional assumption that survival should remain constant over the study period is required. If all larvae spawned in the season are considered as a cohort (year class), this assumption is not required.

The regional study data were used for the mortality analysis because it included the whole estuary and more adequately represented all sizes of larvae. Length was emphasized in analyses rather than age to facilitate the processing of the large number of samples. A range of growth rates for bay anchovy from several sources was used in discussion to enhance comparisons with published rates.

Abundances for 1-mm length intervals were summed over sample weeks. Abundance estimates used in these analyses were adjusted for sampling efficiency as appropriate. Data for bay anchovies were censored to include complete weekly cohorts only. Estimates of length versus age based on otolith analysis for bay anchovy indicated growth of about 3 to 4 mm per week (Table 3). Thus the model was fitted to the data using two censoring schemes: one assuming 3-mm growth per week, and one assuming 4-mm growth per week. The mortality model was estimated

Table 4
Average weekly salinity (ppt) in the Patuxent River. NS = No salinity measurement.

	Segment								
Week	4–7	8–11	12–13	14–17	18–21	22–25	26–29	30–33	34–35
6/01/87	3.0	5.0	NS	10.0	10.0	11.5	13.0	12.5	13.5
6/08/87	0.8	1.0	7.3	11.3	11.0	12.0	13.0	13.0	13.5
6/15/87	2.5	6.5	10.0	11.5	12.5	12.5	12.8	13.0	13.3
6/22/87	3.8	3.8	9.3	11.0	11.8	12.8	13.0	13.5	14.0
6/29/87	2.0	4.5	8.8	10.5	11.3	12.5	12.5	13.0	12.3
7/06/87	2.0	5.0	9.8	11.5	12.0	12.5	13.0	13.0	13.8
7/13/87	4.0	5.5	10.0	11.3	12.3	12.8	12.8	13.0	13.0
7/20/87	2.3	4.5	9.0	10.3	11.5	11.5	12.3	12.3	11.8
7/27/87	5.3	6.0	10.3	11.8	12.8	13.0	13.0	14.3	14.5
8/03/87	6.0	6.5	10.8	12.0	12.8	12.8	12.8	12.8	13.0
8/10/87	7.5	8.0	11.0	11.8	12.3	12.8	12.5	13.0	13.0
8/17/87	5.0	6.8	10.8	12.0	12.8	12.8	11.5	12.5	13.0

using the nonlinear regression procedure of SAS Institute (1985).

Results

Distribution and Migration

Vertically averaged salinity at the mouth of the river ranged from 11.8 to 14.5. ppt. Salinity upriver was more variable; in segments 4 to 7 salinity ranged from 0.8 ppt in June to 7.5 ppt in August (Table 4).

Anchovy spawning occurred further up river as the season progressed. Egg densities in 1987 showed an interaction between river longitude and date ($P = 0.001$). From 29 June to 13 July, greatest densities were in the lower and middle portions of the estuary. During the week of 20 July, densities became more uniform in the river. By 27 July and 3 August, the trend had reversed and the greatest densities were upriver (Table 5). A similar trend was observed for newly hatched larvae. In spite of this shift in densities, standing crops of eggs and newly hatched larvae upriver remained low because of the small river volume in the upper portion of the estuary (Table 6).

Table 5
Mean densities (Mean log (density + 1) per 100 m^3) of bay anchovy eggs and newly hatched larvae in the Patuxent River.

	Section		
Week	Upper	Middle	Lower
Eggs			
6/29/87	2.7	6.9	6.8
7/06/87	2.6	6.7	6.9
7/13/87	1.7	6.5	7.2
7/20/87	3.0	5.8	6.6
7/27/87	4.3	4.3	6.2
8/03/87	5.5	3.1	4.3
Larvae (2 to 3 mm TL)			
6/29/87	2.1	1.5	3.8
7/06/87	1.1	2.8	5.7
7/13/87	2.6	4.0	4.8
7/20/87	3.3	3.8	5.1
7/27/87	2.6	0.6	3.6
8/03/87	3.5	0.0	0.4

The larval densities from the diel data supported the hypothesis that larvae migrate up the estuary as they grow. The size distribution of larvae collected at the mouth of the estuary was compared to those collected in the upper portion of the estuary. Densities of 2- to 3-mm TL larvae were greater ($P<0.05$) in the lower segment (Table 7), whereas densities of each of the 4-mm size classes between 8 to 25 mm were greater upriver. These differences were the same for day and night collections. There were no significant differences in densities of larvae 4 to 7 mm.

Viewing the distribution by 3-mm size classes, there was a single large mode for the smallest sized larvae at the mouth of the estuary (Fig. 2); whereas upriver there were two modal lengths, one of small larvae associated with the late season spawning and another at 20-mm TL.

This trend was more pronounced in the standing crop estimates based on data from the regional study. A plot of mean standing crops for bay anchovy larvae versus length for the three sections of the Patuxent River (Fig. 3) showed that the standing crop of small larvae found in the lower section of the estuary was several orders of magnitude greater than the number found in the middle and upper sections. This high standing crop of small larvae in the lower section resulted from high densities com-

Table 6
Estimated standing crops (millions) of bay anchovy eggs and newly hatched larvae in the Patuxent River.

Week	Section		
	Upper	Middle	Lower
Eggs			
6/29/87	371	3263	5470
7/06/87	15	2742	7384
7/13/87	60	4800	6371
7/20/87	89	2889	8378
7/27/87	620	589	2323
8/03/87	328	124	469
Larvae (2 to 3 mm TL)			
6/29/87	7	29	619
7/06/87	4	241	2076
7/13/87	8	533	753
7/20/87	39	220	2530
7/27/87	16	5	313
8/03/87	14	0	5

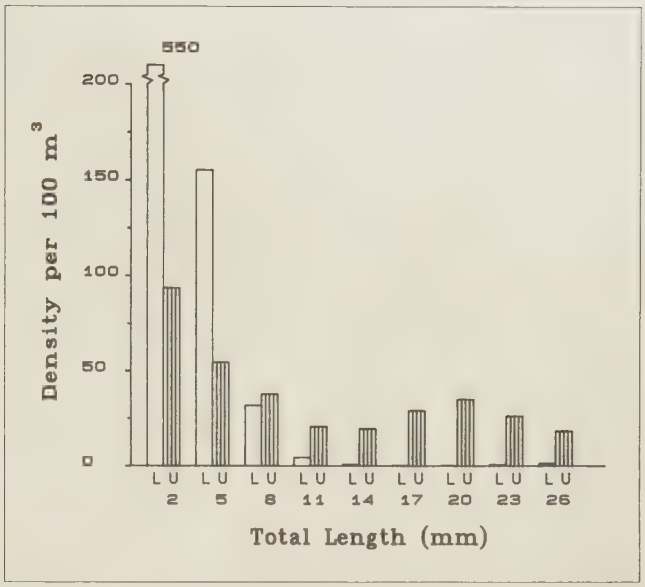

Figure 2
Comparison of length-density distributions of bay anchovy larvae at the lower (L) and upper (U) part of the river.

Table 7
Mean diel densities (Mean log (density + 1) per 100 m^3) of bay anchovy larvae in the Patuxent River at upriver stations versus downriver stations averaged over depth layers and over the sampling season.

Total length (mm)	Day		Night	
	Upriver	Downriver	Upriver	Downriver
2–3	2.06	3.76	1.99	2.60
4–7	2.68	3.07	2.74	2.72
8–11	2.75	1.67	2.56	1.84
12–15	2.00	0.38	2.18	0.60
16–19	1.37	0.04	2.05	0.24
20–23	1.36	0.02	2.19	0.36

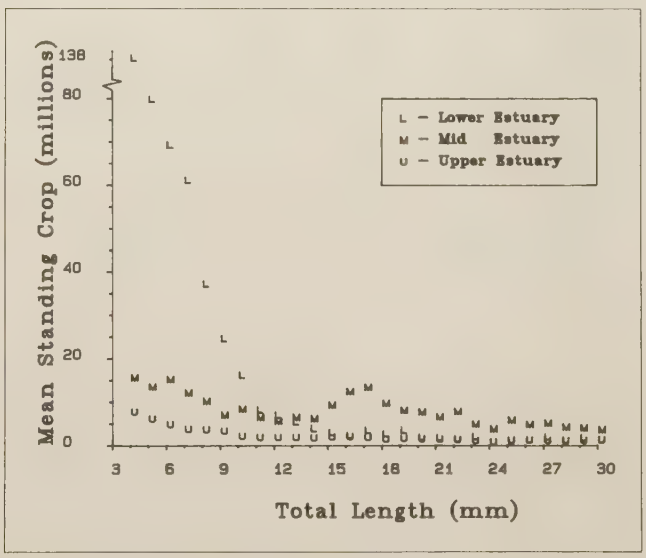

Figure 3
Mean standing crop estimates for bay anchovy larvae for three portions of the Patuxent River estuary in 1987.

bined with the large volume of that portion of the estuary (Tables 1 and 8). Numbers of large larvae, on the other hand, were greatest in the middle section of the estuary.

An evaluation of the vertical distribution of larvae indicated that at the mouth of the river larvae of lengths less than 12-mm TL remain in deep water during day and night ($P<0.05$) (Table 9). Larvae in each length class greater than 11-mm TL showed no significant vertical patterns downriver. In contrast, in segments 10 to 14, during the day larvae in each length class greater than 8 mm were near the surface ($P<0.05$) layer while at night larvae in each length class greater than 11 mm were near the bottom layer ($P<0.05$). The smaller larvae did not exhibit vertical patterns in the upper river.

Mortality

The parameter estimates for a range of growth rates are:

3 mm/week	4 mm/week
α = 1.7631	α = 3.4505
β = 1.0375	β = 1.3320
c = −37.5911	c = 0.7849.

Table 8

Average densities per 100 m^3 of bay anchovy larvae (>3 mm TL) in the Patuxent River and the adjacent portion of Chesapeake Bay. NS = Not sampled.

	Segment[a]										
Week	4–7	8–11	12–13	14–17	18–21	22–25	26–29	30–33	34–35	35	Bay
Larvae (4 to 9 mm TL)											
6/01/87	0	10	0	0	0	0	0	0	0	NS	NS
6/08/87	0	10	10	0	0	0	0	0	0	NS	NS
6/15/87	0	10	0	0	10	0	10	0	20	10	NS
6/22/87	20	0	0	0	10	30	20	30	40	NS	NS
6/29/87	40	30	110	20	30	20	30	130	300	210	720
7/06/87	40	40	40	20	10	50	80	250	590	NS	250
7/13/87	50	30	20	50	60	200	100	170	520	570	1450
7/20/87	50	220	70	150	90	130	150	270	480	NS	520
7/27/87	520	360	70	40	10	10	20	50	170	120	90
8/03/87	120	280	20	10	0	0	30	30	40	NS	30
8/10/87	90	50	10	0	0	0	10	10	0	0	0
8/17/87	170	330	110	10	0	0	0	0	20	NS	0
Larvae (>9 mm TL)											
6/01/87	0	10	0	0	10	0	0	0	0	NS	NS
6/08/87	20	10	20	0	0	0	0	0	0	NS	NS
6/15/87	0	10	0	10	0	0	0	0	0	0	NS
6/22/87	20	10	20	20	0	20	0	0	10	NS	NS
6/29/87	10	30	70	150	20	10	0	10	0	0	150
7/06/87	50	130	280	170	0	20	20	20	40	NS	20
7/13/87	60	140	80	960	70	80	10	30	0	10	60
7/20/87	50	60	190	420	60	40	80	50	40	NS	50
7/27/87	130	130	220	220	110	70	20	30	50	40	20
8/03/87	100	160	160	480	270	100	110	20	60	NS	40
8/10/87	90	220	110	150	120	30	20	10	20	50	0
8/17/87	170	240	150	280	80	40	60	50	0	NS	0

[a]Estimates for segment 35 are from the diel study (averaged over day and night periods). Estimates for other segments are from the regional study and have been adjusted for sampling efficiency.

Table 9

Vertical diel distributions (Mean log [density + 1] per 100 m^3) of bay anchovy larvae in two portions of the Patuxent River averaged over the sampling season.

		Depth zone (m)					
		Upriver portion of Patuxent River			Mouth of Patuxent River		
Length (mm)	Diel period	0–1	1–2	>2	0–1	1–3	>3
2–3	Day	1.66	2.21	2.40	2.88	3.36	4.61
	Night	1.84	2.03	2.14	1.97	2.31	3.23
4–7	Day	2.68	2.85	2.44	2.57	2.62	3.71
	Night	2.58	2.68	2.03	2.20	2.29	3.36
8–11	Day	3.13	2.73	2.26	1.23	1.46	2.10
	Night	2.37	2.70	2.61	1.20	1.62	2.44
12–15	Day	2.51	1.97	1.34	0.32	0.31	0.47
	Night	1.65	2.40	2.60	0.26	0.61	0.83
16–19	Day	2.46	1.00	0.35	0.00	0.07	0.04
	Night	0.96	2.53	2.85	0.17	0.51	0.10
20–23	Day	2.21	1.23	0.38	0.06	0.02	0.00
	Night	1.19	2.52	3.08	0.23	0.37	0.44

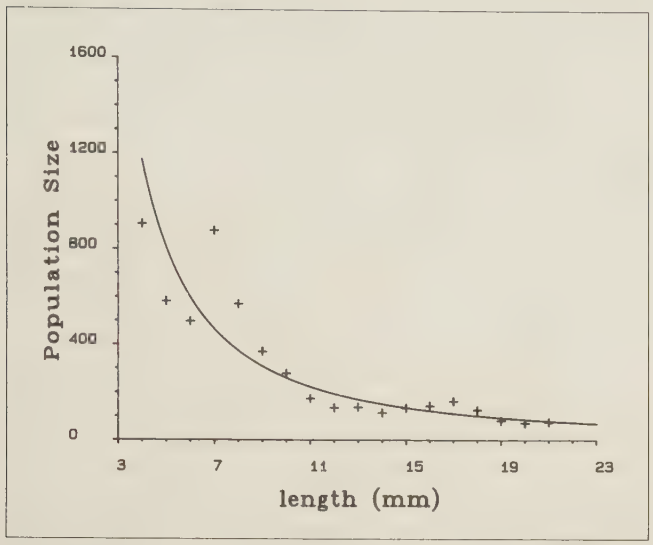

Figure 4
Mortality curve with respect to length for bay anchovy using 1987 data censored according to 3 mm/week growth and the observed abundances from which the curve was estimated.

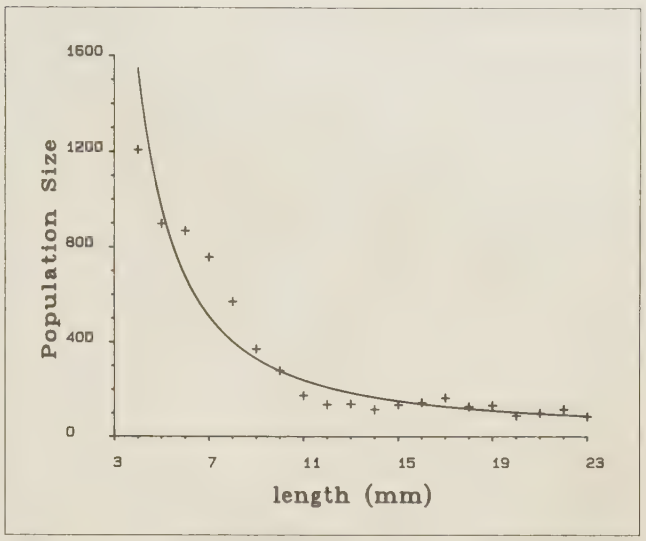

Figure 5
Mortality curve with respect to length for bay anchovy using 1987 data censored according to 4 mm/week growth and the observed abundances from which the curve was estimated.

The fit of the curve assuming 4 mm growth per week was better than one assuming 3 mm growth per week (Figs. 4 and 5).

Estimated mortality rates per individual ($\alpha L^{-\beta}$) based on these curves ranged from 0.161 to 0.162 per mm of growth at 10 mm TL and from 0.064 to 0.079 per mm of growth at 20 mm TL. These rates correspond to 15% per mm at 10 mm TL and 6.2% and 7.6% per mm at 20 mm TL.

Discussion

Sampling Considerations

Information from the random stratified sampling design implemented in this study was used to address the hypothesis that bay anchovy eggs are spawned downriver and the young larvae move upriver to a nursery area. To analyze changes in abundance, vertical, longitudinal, and temporal stratification was required. Randomly selecting sampling locations within strata satisfies the underlying assumptions of hypothesis testing through ANOVA.

The importance of sampling a broad spectrum of strata can not be overemphasized. For example, the geographic area considered by Polgar et al. (1988) excluded the lower section of the Patuxent River estuary. Their estimate of the mortality rate for postlarval bay anchovies in the Patuxent River in 1978 (0.016 per tidal cycle or 0.032 per day) was considerably less than our range of estimates. Our data ("lower estuary" in Figure 3) show that excluding data from this section of the estuary leads to an underestimate of mortality.

Furthermore, when making population assessments, it is important to consider the volumes of the river segments. Early studies in the Patuxent River estuary (Dovel 1971) considered only density data. Note that the density of large larvae upriver seems relatively high, but the volumes of upriver segments are relatively small. If one considered larval density only, larval mortality would be underestimated and the extent of upriver migration would be overestimated.

Distribution and Migration

The longitudinal distribution of the eggs indicates that spawning occurs primarily in the lower section of the river. Collections in the Patuxent River in 1978 by Setzler et al. (1979) did not extend below segment 20, but the distribution pattern for eggs is consistent with the data for 1987 in that the highest densities were found downriver. The late season spawning observed upriver in 1987 may have been partially associated with an increase in salinity. Salinity in the upper river segments increased approximately 2 ppt during the period 20 July to 3 August (Table 4).

From the pattern of many small larvae and few large larvae downriver opposed to relatively more large larvae and few small larvae upriver (Fig. 2) we infer either that the larvae hatch downstream and migrate upriver or that the larvae suffer much greater mortality downriver than upriver. However, the differential mortality argument is not sufficient to explain the data. For any cohort abundance is a monotonically decreasing function of length or age. Thus the sum or average of cohort abundances also has this property. For the upriver segment, the number

of larvae with lengths 17 to 23 mm TL averaged over the spawning season (i.e. averaged over cohorts) actually exceeded the number of larvae with lengths 8 to 14 mm. Since it is impossible to explain this phenomenon solely by differential mortality, one must conclude that the increase in density of 17 to 23 mm larvae upriver resulted wholly or partially from migration of larvae from downriver.

This same issue is examined in terms of avoidance corrected abundance (Fig. 3) with data from three sections of the river. It is clear that there were more larvae in the middle section (segments 14 to 25) in the 15 to 21 mm length category than can be explained without invoking migration from the lower section (segments 26 to 35). Small larvae originate in the lower third of the estuary and move to the middle section of the estuary as they grow. Few larvae enter the upper section (segments 4 to 13) of the river.

While the data indicate that larval migration occurred, the mechanism for the migration is not clear. Many studies have found that larvae use water currents to move to nursery areas (Norcross and Shaw 1984; Weinstein 1988). Current velocity estimates for tidally averaged water flow in the Patuxent River indicate upriver flow in deeper water (ANSP 1983; Edinger et al. 1989). Thus the vertical position of larvae will determine the direction of transport based on the net direction of flow at that vertical position. Since small larvae downriver remain in lower depths, they could be transported to their nursery areas upriver with baroclinic circulation.

Mortality

We use a model based on the simple but appealing assumption that larval mortality rate decreases with increasing length. Swimming speed and thus ability to avoid predators is a direct function of length rather than age (Fuiman and Webb 1988) The mortality rate is believed to be greatest for eggs and very small larvae because they are unable to avoid predation. Larger larvae should be better able to obtain food and avoid predators and their survival should be greater. Other assumptions of this application need to be examined.

Use of length as a surrogate for age is justified because of the close correspondence between length and age (Fives et al. 1986; Leak and Houde 1987). The logic is that if survival = g(time) and length = f(time) then survival = $g(f^{-1}$ (length)). For convenience the plot of abundance versus length is referred to as a "survival curve" or a "mortality curve."

Immigration/emigration of bay anchovy larvae $\geq$10 mm TL would not be expected to be a major source of error in mortality estimates because densities at the mouth of the river are relatively low compared to densities in the middle portion of the study area (Table 8). Our data suggest that juvenile bay anchovies ($\geq$23 mm TL) move down river, but these were not included in our mortality analysis. In contrast, one would expect that small larvae would be transported into the river because of high densities in deeper layers at the mouth of the river. This would cause an underestimation of mortality for these small larvae. An evaluation of the emigration of small larvae from Chesapeake Bay requires further study.

Based on published results, we have assumed a growth rate of 3 to 4 mm per week (Table 3). With cohorts defined by using length classes approximately equivalent to one weeks growth, weekly sampling is sufficient to represent all cohorts of the spawning season.

This model was motivated by finding that the commonly used constant mortality rate model (Houde 1987; Leak and Houde 1987) was inadequate for these data. Residual plots for our data indicated that a constant rate model underestimated mortality for small larvae and overestimated mortality for large larvae. The Weibull mortality model can be used for modeling increasing or decreasing mortality rate curves (Pinder et al. 1978). The Weibull model has been employed for modeling a decreasing mortality rate in a larval fish population (Saila and Lough 1981). However, use of the Weibull model seems to be founded on empirical curve fitting rather than biological assumptions. We prefer a model founded on the commonly observed phenomenon that mortality decreases with increasing length (Ware 1975; Hackney 1977; Saila and Lough 1981).

As noted, we may have underestimated mortality of larvae $<$10 mm TL because the immigration of these small larvae into the river from the Chesapeake Bay was not taken into account. Thus the difference in mortality rates between large and small larvae may have been even larger than we estimated. If this is the case, there is even greater need for a decreasing mortality model.

The Pareto model is also applicable when ages of larvae are known. Lo (1985) used an age-based Pareto model for eggs and larvae of northern anchovy. The length-based Pareto model presented here can also be used. One need only substitute the growth equation for length in the denominator of the first differential equation and perform the calculus to obtain a model based on age which uses the same assumptions. If the growth equation is assumed linear, a simple substitution of the growth equation in the final model yields

$$\log_e (N_t) = \frac{-\alpha}{1-\beta}(h + gt)^{(1-\beta)} + c. \qquad (7)$$

The expression $(h + gt)$ is a linear model for length as a function of age, where t = age
h = hatching size
g = growth rate.

This equation indicates that the number of surviving larvae at age t increases as hatching size and growth rate increase. The importance of hatching size and growth rate

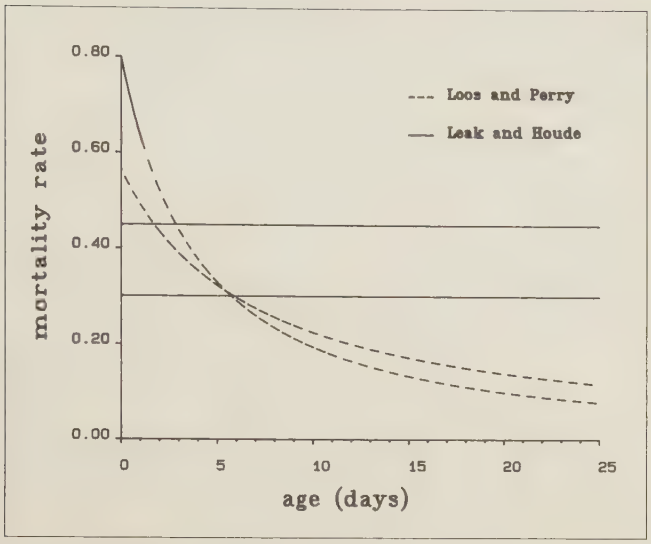

Figure 6
Constant mortality rates published by Leak and Houde (1987) compared to decreasing mortality rates published here. The two solid curves show the range of values reported by Leak and Houde. The two dashed lines show the range of values that result from using 3 and 4 mm/week growth rates in this study.

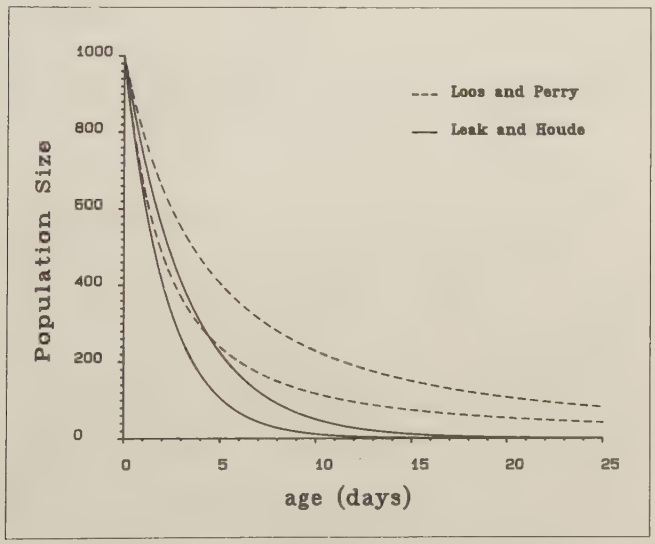

Figure 7
Survival curves with respect to age for bay anchovy larvae estimated here compared to those computed from estimates by Leak and Houde (1987). The two solid curves show the range of values reported by Leak and Houde. The two dashed lines show the range of values that result from using 3 and 4 mm/week growth in this study.

in the evaluation of mortality has been emphasized by Ware (1975) and Houde (1987), respectively.

The mortality rate derived here is compared to a constant mortality rate estimated for larval bay anchovies in Biscayne Bay by Leak and Houde (1987). The Pareto function is transformed to a function of age by compositing the mortality with respect to length function with a length with respect to age function. Two growth rates for the Patuxent River, 3 mm/week and 4 mm/week, are used for comparison. Mortality rates for the Pareto model are greater than the constant estimates for larvae less than two days old and become less than the constant mortality rates for larvae greater than five days old (Fig. 6). As a result the net mortalities estimated by the Pareto model for the Patuxent River are much less by the time larvae are eight days old (Fig. 7).

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Hypothetical Northern Spawning Limit and Larval Transport of Spot*

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ABSTRACT

The exact northern limit of the spawning grounds of spot (*Leiostomus xanthurus*) has not been determined. Previous reports of spot spawning during the winter/spring in the Middle Atlantic Bight (MAB) are refuted based on the presence of low bottom-water temperatures at that time. Analyses of historic bottom isotherms in the MAB during winter/spring show that the most northerly occurrence of required 17°C bottom temperatures from December to May is on the outer continental shelf off North Carolina near the Gulf Stream. It is therefore suggested that spot recruiting to Chesapeake Bay are spawned near Cape Hatteras at the shelf break in winter. A mechanism must then exist to transport larvae approximately 250 km northward in the MAB before recruiting to Chesapeake Bay one to three months later. Episodes of southerly winds, interspersed between seasonal spring northerly winds, were identified from 1978 through 1988. These southerly winds could cause current reversals over the inner shelf areas of the MAB and may transport waves of new spot recruits northward from the southern spawning site. These winds may have been related to waves of juvenile spot recruiting to Virginia estuaries in 1987 and 1988. The duration and frequency of southerly wind events during the months when larvae are being transported could have a major impact on year-class success.

Introduction

Spot (*Leiostomus xanthurus*) is a common sciaenid along the middle and southern Atlantic and Gulf coasts of the United States. They appear to have a protracted spawning season which probably begins in September and ends in April or May with reported times varying with location (Hildebrand and Cable 1930; Dawson 1958; Lewis and Judy 1983). It has been suggested that spawning occurs off Chesapeake Bay from late fall through early spring (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Lippson and Moran 1974). The season extends from October through March off the coasts of North and South Carolina (Dawson 1958) with peak spawning occurring in December and January (Hildebrand and Cable 1930; Dawson 1958; Berrien et al. 1978; Lewis and Judy 1983; Warlen and Chester 1985).

In fall, spot are generally distributed in the Middle Atlantic Bight (MAB) nearshore from Long Island, NY to Cape Lookout, NC (NMFS/NEFC 1983-87). In the winter, from Cape Hatteras to central Florida, spot may move offshore to occupy the shelf edge (Manooch and Raver 1984). Although spot have been recorded from depths of 165 m (Squire 1958) and 204 m (Springer and Bullis 1956), they are usually found in depths less than 100 m (Pearson 1932; Dawson 1958). Spot tagged in Chesapeake Bay (Pacheco 1962) and Delaware Bay (Pearson 1932) were returned by trawlers operating south of Cape Hatteras, NC in winter. This suggests that spot from these northern areas may have a common coastal feeding or spawning ground during winter (Chao and Musick 1977). There are so few spot captured in the MAB in the spring that the species is not reported by groundfish cruises (NMFS/NEFC 1984-88) undertaken in March, lending further support for a common winter ground offshore or south of Cape Hatteras.

Since spawning has not been observed, many conclusions about spawning time and place are based on collections of larvae and juveniles (Hildebrand and Cable 1930; Lewis and Wilkens 1971; Berrien et al. 1978; Lewis and Judy 1983). Spawning probably occurs on the mid to outer continental shelf (Warlen and Chester 1985) over deeper

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Table 1
Literature records of initial spot recruitment dates and sizes in Chesapeake Bay.

Spot reference	Place	Date	Size (mm)
Welsh and Breder 1923	Chesapeake Bay	Jan.–April	19–37
Hildebrand and Schroeder 1928	Chesapeake Bay	1st wk March	15–19
Pacheco 1957	York River	April	15–22
Pacheco 1962	York River	April/May	22–85
Richards and Castagna 1970	eastern shore	May–Sept.	21–99
Chao and Musick 1977	York River	Early April	14–45
Schauss 1977	Lynnhaven Bay	April	—
Orth and Heck 1980	Chesapeake Bay	March	—
Olney 1983	Chesapeake Bay	Feb./March	11–20
Weinstein and Brooks 1983	Chesapeake Bay	April	20
Heck and Thoman 1984	York River	April	—
McCambridge and Alden 1984	James River	April	16–22
Smith et al. 1984	York River	April	—
Cowan and Birdsong 1985	Wachapreague	April/May	15–33
O'Neill and Weinstein 1987	York River	April	—
Olney and Boehlert 1988	Chesapeake Bay	April/May	—
Seigfried 1989	York River	April	14–19

bottoms (Dawson 1958). Off North Carolina, the size and age of spot larvae increased from offshore toward the coastline (Lewis and Judy 1983; Warlen and Chester 1985). Primarily, time of spawning has been inferred from time of juvenile recruitment to the estuaries. Juveniles recruit to Georgia estuaries from February through April (Rogers et al. 1984) and to South Carolina from January through June (Beckman and Dean 1984; McGovern 1986), peaking in February (McGovern 1986). Recruitment to North Carolina may occur October through March, but appears to be concentrated from January to March (Tagatz and Dudly 1961; Williams and Deubler 1968; Lewis and Mann 1971; Turner and Johnson 1973; Lewis and Judy 1983). Spot are approximately two months of age when entering estuaries in North Carolina (Warlen and Chester 1985) and South Carolina (Beckman and Dean 1984). Recruitment to Chesapeake Bay usually occurs in April and May (Table 1) but has been reported as early as January (Welsh and Breder 1923), February (Olney 1983), or March (Hildebrand and Schroeder 1928; Orth and Heck 1980). Variation in time of juvenile recruitment indicates a change in time or place of spawning or in mechanisms responsible for transport of larvae to inshore nurseries.

These observations indicate that spot spawn over the mid to outer shelf, inshore of the Gulf Stream, from at least North Carolina southward. However, since spot recruit to Chesapeake Bay as post-larvae or juveniles in the spring, it has been concluded that spawning also takes place as far north as the Chesapeake area of the MAB (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Johnson 1978; Lippson and Moran 1984). Mechanisms responsible for transport of larvae from the spawning ground to the nursery have not been investigated. It is the intention of this paper to analyze historic and recent data to formulate hypotheses which exclude the MAB (Fig. 1) as a spawning location and propose theoretical transport pathways from a southerly spawning site to Chesapeake Bay. Additionally, we will suggest direction for future investigations to test these hypotheses.

Methods

Bottom isotherms were obtained from the National Marine Fisheries Service (NMFS)/Northeast Fisheries Center (NEFC) bottom-trawl survey cruise publications (Edwards et al. 1962; Davis 1979; Nickerson and Wright 1980; NMFS/NEFC 1983–1988) or as unpublished plots (L. Lierheimer, NMFS/NEFC, Woods Hole, MA 02543, December 1987). Bottom temperatures (°C) from cruises 8701 (February–March 1987), 8801 (February 1988), and 8901 (February–March 1989) were collected aboard the NOAA ship *Ferrel* by the authors. Because laboratory studies of spot show spawning to take place between 17.5°C and 25.0°C (Hettler and Powell 1981), the 17°C isotherm was selected as an index of spawning temperature. Bottom water temperatures were examined between 39°N and 33.5°N latitude (Fig. 2A) from November through May, 1965–1989. Data were aggregated seasonally based on timing of most collections and applicability to spot life history: November–December, January–February and March–May (Table 2).

Wind data from Norfolk International Airport, Virginia has previously been validated for application in the MAB (Norcross and Austin 1988). Daily resultant wind speed and direction for 1978–1988 (National Weather Service,

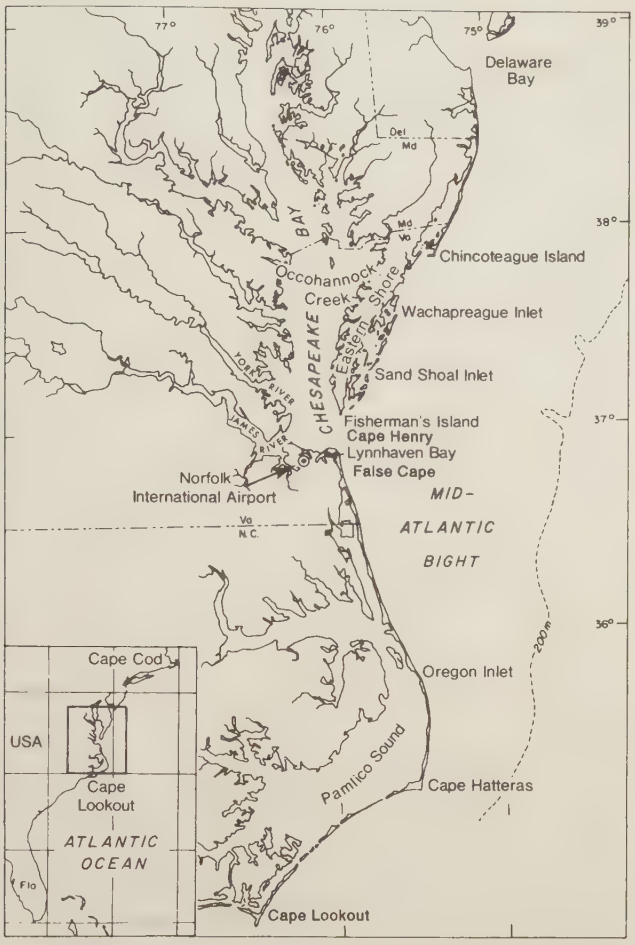

Figure 1

The area of study on the east coast of the United States including the Middle Atlantic Bight and Chesapeake Bay. Note: southern extent of bottom temperatures collected on NMFS cruises (Table 2): Chincoteague Island (38° N), Chesapeake Bay mouth (37° N), Oregon Inlet (36° N), and Cape Hatteras (35° N). Sites of collections of juvenile spot on the eastern shore of Virginia, (Wachapreague Inlet, Sand Shoal Inlet, and Fisherman's Island), and within Chesapeake Bay, (Occohannock Creek, York River, James River, and Lynnhaven Bay). Norfolk International Airport, site of recording of wind data.

1978–88) were processed by smoothing with seven-day running averages which corresponded to the physical time range applicable for transport in the South Atlantic Bight (Yoder 1983). The daily resultant winds were analyzed for the time period from November through June, the time of spawning and recruitment of spot to Chesapeake Bay. The total number of southerly wind events (i.e., the number of wind vectors having a northward component) and the number of southerly events lasting four consecutive days were compared for different years and months.

Ichthyoplankton samples were collected near the shore to 200 m offshore in the southern MAB as far north as New Jersey and as far south as Cape Lookout, NC. Larvae were collected by stepped oblique tows using Gulf-V samplers aboard the RV *Dolphin* in 1965 and 1966 (Berrien et al. 1978). Later collections of spot larvae (1977–1986), available from NMFS/NEFC cruises (M. Fahay, NMFS/NEFC, Highlands, NJ 07732, pers. commun. Nov. 1988), used double oblique bongo-net tows following standard MARMAP guidelines (Jossi and Marak 1983). These sampling techniques do not yield information on the vertical distribution of larvae. The horizontal distribution of larval spot was plotted for November–December, January–February, March, April, and May by combining data from all cruises. The mean length of larvae was calculated for each station. Station locations from each cruise did not overlap since those from the RV *Dolphin* were located on transects perpendicular to the coastline and those from the NMFS/NEFC cruises were selected by stratified random sampling techniques.

As part of a larger study, estuarine areas within Chesapeake Bay and locations in lagoons on the seaside of Virginia's eastern shore were sampled twice monthly from September 1986 through August 1987 and monthly from September 1987 through August 1988. Sample locations consisted of Wachapreague Channel and Inlet (five stations) Sand Shoal Channel and Inlet (five stations) and Fisherman's Island (one station) on the seaside of the Virginia eastern shore; Occohannock Creek (four stations) on the bayside of the eastern shore; and the mouth of the York River (eight stations) on the west side of Chesapeake Bay (Fig. 1). Stations were located in channels of creeks and rivers and directly behind the barrier islands, and in shallow areas within the marsh complex. Sites were similar with regard to depth, proximity to houses and creek size. Weather permitting, two samples were taken at all 23 stations on each of 36 trips. A 4.9-m semi-balloon trawl with a codend mesh of 6.4 mm and a 3.2-mm codend liner was used at 18 of the stations. At the other five stations, one at each site, a 6.1-m bag seine with a 3.2-mm mesh was used (Norcross and Hata, in press). All spot captured were preserved in either 10% formalin or 95% ethanol and returned to the laboratory where they were measured to the nearest 1 mm increment of total length (TL).

Results and Discussion

Examination of 48 sets of bottom isotherms—10 for November–December, 14 for January–February, and 24 for March–May (Table 2)—produced plots of the 17°C isotherm by season (Fig. 2A). Water as warm as 17°C is present in the MAB during November–December, but the location exhibits interannual variation in position. Rarely is there any water as warm as 17°C present in winter. Of the 14 sets of data examined for January–February, there was a very restricted amount of water warmer than 17°C

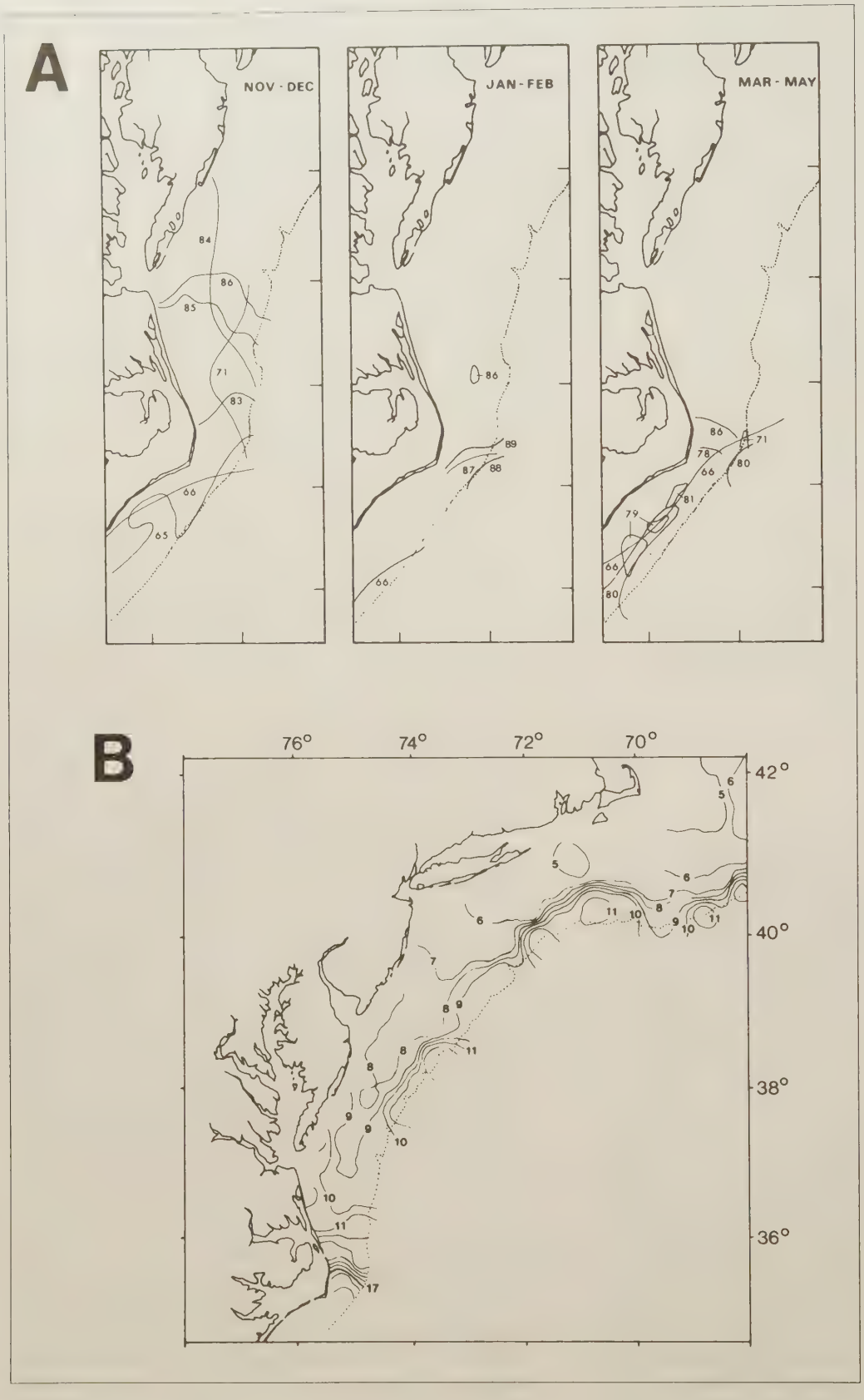

Figure 2
The continental shelf area to 200 m (dotted line) in the Middle Atlantic Bight and around Cape Hatteras. (**A**) Seasonal distribution of the 17° C isotherm. Numbers, located on the side of the isotherm greater than 17° C, indicate the year in which the isotherm was in that position. Source is data in Table 2. (**B**) Bottom water temperatures on 1 May generated from average temperatures of 10 years of NMFS data (D. Mountain and T. Holzwarth, NMFS/NEFC, Woods Hole, MA 02543, unpubl. data 1988).

Table 2

Bottom-water temperature data, 1965–1989 (Davis 1979; Nickerson and Wright 1980; NMFS/NEFC 1983–1988; Norcross and Bodolus, unpub. data.) All cruises started at least as far north as New Jersey; southern extent of cruise track listed here.

Year	Dates	Cruise I.D. #	Southern extent	Highest temp.
		November–December		
1965	3–23 Dec	6504	Cape Lookout	22°C
1966	9 Nov–4 Dec	6614	Cape Lookout	22°C
1971	8–19 Nov	7103	Cape Lookout	24°C
1978	Dec	7807	Chesapeake Bay	16°C
1980	19 Nov–21 Dec	8012	Oregon Inlet	14°C
1982	15 Nov–22 Dec	8209	Chincoteague	14°C
1983	14 Nov–21 Dec	8309	Cape Henry	18°C
1984	29 Nov–7 Dec	8409	Cape Hatteras	24°C
1985	5 Nov–12 Dec	8510	Cape Hatteras	24°C
1986	3 Nov–12 Dec	8610	Cape Hatteras	24°C
		January–February		
1959	23 Jan–3 Feb	126	Cape Hatteras	15°C
1966	26 Jan–9 Feb	6601	Cape Lookout	17°C
1978	Jan–Feb	7801	Oregon Inlet	13°C
1978	16 Feb–17 Mar	7802	Cape Hatteras	12°C
1979	Jan	7901	Chesapeake Bay	10°C
1979	23 Feb–15 Mar	7903	Cape Hatteras	12°C
1980	3 Jan–10 Feb	8001	Oregon Inlet	12°C
1981	17 Feb–24 Mar	8101	Chesapeake Bay	11°C
1984	9 Jan–10 Feb	8401	Chesapeake Bay	12°C
1985	7 Jan–8 Feb	8501	Chesapeake Bay	12°C
1986	7 Jan–12 Feb	8601	Cape Hatteras	17°C
1987	5 Jan–13 Feb	8701	Cape Hatteras	16°C
1987	23 Feb–6 Mar	8701	Cape Hatteras	21°C
1988	8 Feb–26 Feb	8801	Cape Hatteras	18°C
1989	13 Feb–2 Mar	8901	Cape Hatteras	21°C
		March–May		
1966	6–21 Apr	6603	Cape Lookout	21°C
1968	4 Mar–16 May	6803	Cape Hatteras	10°C
1969	5 Mar–10 Apr	6902	Cape Hatteras	10°C
1970	12 Mar–29 Apr	7003	Oregon Inlet	14°C
1971	9 Mar–5 May	7101	Cape Hatteras	18°C
1972	8 Mar–24 Apr	7202	Oregon Inlet	13°C
1972	20–31 Mar	7208	Cape Lookout	20°C
1973	16 Mar–15 May	7303	Oregon Inlet	11°C
1974	12 Mar–4 May	7404	Oregon Inlet	14°C
1975	14 Mar–12 May	7503	Oregon Inlet	10°C
1976	4 Mar–5 May	7605	Oregon Inlet	12°C
1977	19 Mar–27 Apr	7703	Oregon Inlet	11°C
1978	20 Mar–25 May	7804	Cape Hatteras	14°C
1978	Apr–May	7804	Cape Hatteras	17°C
1979	20 Mar–12 May	7904	Cape Lookout	18°C
1979	6–19 May	7904	Cape Hatteras	20°C
1980	29 Feb–4 Apr	8002	Cape Hatteras	18°C
1980	16 Mar–2 May	8003	Cape Lookout	18°C
1981	17 Mar–14 May	8100	Cape Lookout	17°C
1981	18 Mar–9 Apr	8103	Cape Hatteras	11°C
1981	20 May–18 Jun	8103	Chincoteague	12°C
1985	1 Apr–2 May	8303	Cape Hatteras	14°C
1986	6 May–7 Jun	8603	Cape Hatteras	19°C
1987	5 May–8 Jun	8704	Oregon Inlet	11°C

available in only five of the 12 years. While 17°C water was available in March–May, it was restricted to near Cape Hatteras (Fig. 2, A and B). There is a convergence zone near Cape Hatteras which causes a dramatic increase in bottom water temperature (Bumpus 1973). This zone forms in the autumn, persists throughout the winter, and breaks down in the spring (Bumpus et al. 1973). Remnants of this convergence zone can be seen in the March–May bottom temperatures (Fig. 2A), with water warmer than 17°C present in almost half of the years. Ten years of data taken by NMFS/NEFC cruises show this convergence zone at Cape Hatteras on 1 May (Fig. 2B).

Based on these bottom temperature distributions, we conclude that spot do not spawn in the MAB in winter, rather that they spawn near or south of Cape Hatteras where the water temperature is 17°C or higher. Spot could theoretically spawn in the MAB in November and early December when water warmer than 17°C is still present. However, since spot do not recruit to Chesapeake Bay until March and April (Table 1), it seems unlikely they they would spawn in the fall as that would require a mechanism to keep the larvae offshore in the MAB for four to six months.

If spot are spawning at the shelf break near Cape Hatteras in winter and spring, as indicated by bottom water temperatures, then a mechanism must exist to transport the larvae northward on the shelf from Cape Hatteras towards Chesapeake Bay. The mean longshore flow in the MAB, however, is southerly (Bumpus 1973). This mean flow decreases from a maximum near the shelf break toward the coast where the shallow inner shelf is prone to wind-driven forces (Beardsley and Boicourt 1981).

Eggs and larvae of spot are pelagic (Powell and Gordy 1980), though their depth distribution is unknown, and thus subject to transport by winds and currents. Year-class strength seems to vary yearly and to be determined by time of recruitment to the estuary (Joseph 1972). These non-periodic year-to-year fluctuations are thought to be caused by environmental differences that occur on the spawning ground (Joseph 1972). Extended periods of offshore-directed winds during the pelagic phase may cause drastic reductions in a year class (Manooch and Raver 1984).

Vectors of seven-day running averaged winds from Norfolk International Airport for 1978–1988 show strong northerly winds from October through April with episodes of southerly winds from January onward. May and June show a seasonal shift to predominantly southerly winds (Fig. 3). These episodes of seasonal wind reversal could cause current reversals in the MAB (Bumpus 1973) and serve as a transport mechanism for spot recruiting to Chesapeake Bay. The number of southerly wind events and the number of southerly wind events lasting four consecutive days (Fig. 4) were analyzed for differences between months and years. There was no significant difference

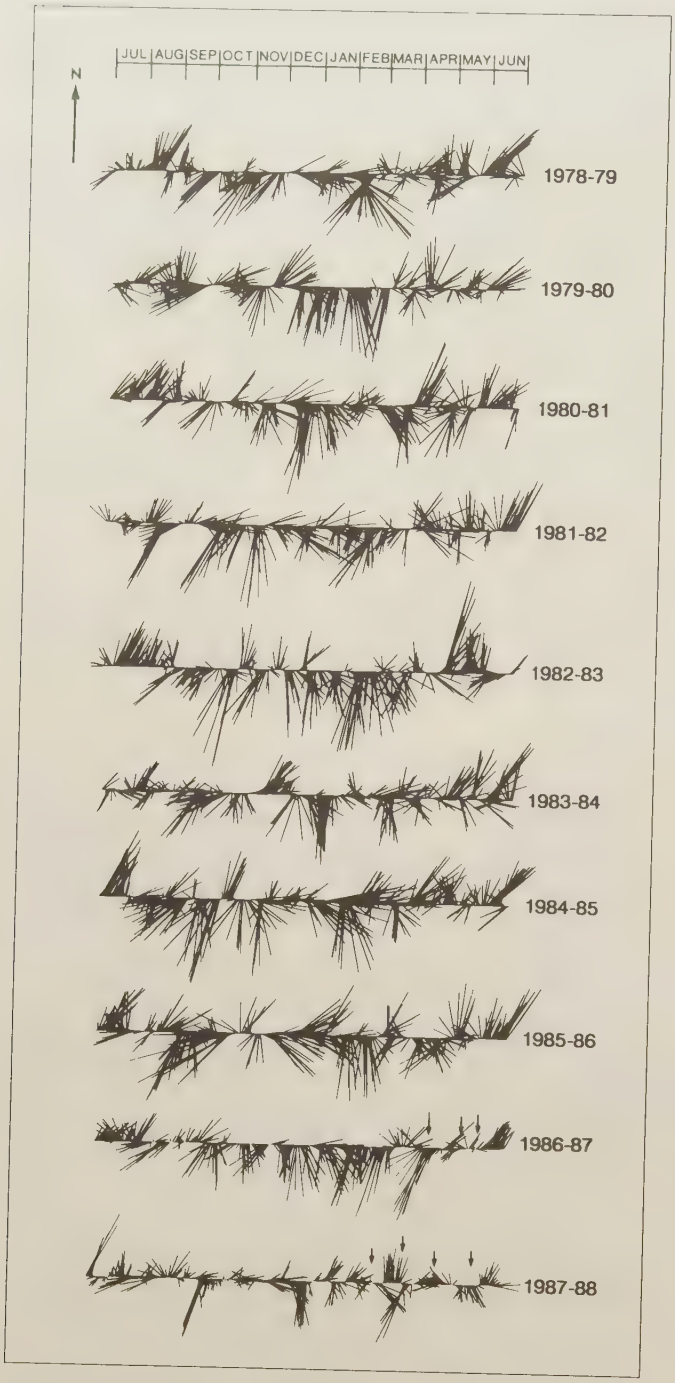

Figure 3
Wind vectors from Norfolk International Airport, Virginia, (1978–1988) were processed by smoothing with 7-day running averages. Time scale is 1 July through 30 June of the following year. Up is north. Orientation is in the direction towards which the wind is blowing, i.e., away from the center line. Note southerly events occurring from December to March. Arrows indicate appearance of cohorts of juvenile spot in the Chesapeake Bay estuaries in 1987 and 1988 (Figures 6 and 7).

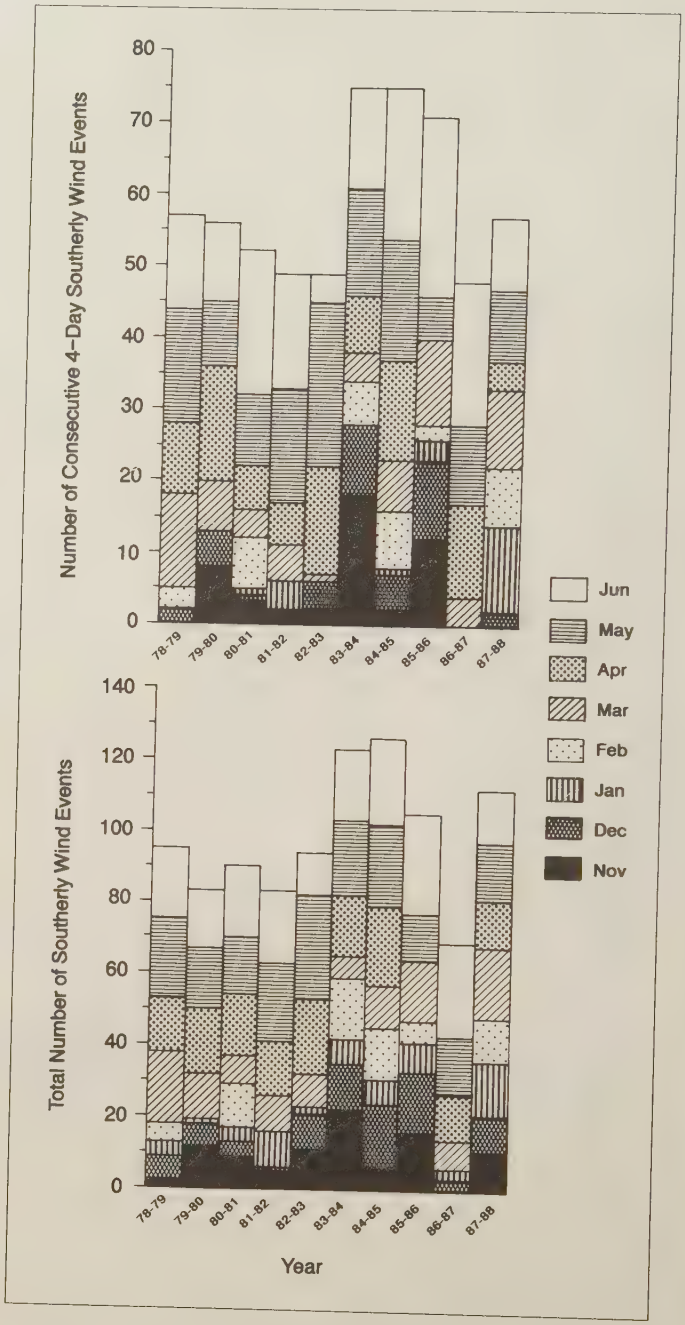

Figure 4
Total number of southerly wind events and number of consecutive 4-day southerly wind events taken from vector plots in Figure 3.

between years in number of southerly winds of either type occurring between November and June. However, the total number of southerly events ($F = 10.3$; df = 7,63; $P<0.01$) and the number of four-day southerly events ($F = 9.6$;

df = 7,63; $P<0.01$) occurring per month were significantly different.

As expected, the total number of southerly events per year is constant. It is the timing of these southerly events relative to periods when larvae are pelagic that is most important. Spot larvae begin entering Chesapeake Bay primarily during March and April. If these fish are approximately two months of age as found in North and South Carolina, then the time frame for wind analysis needs to be narrowed to those months where wind events are most likely to affect the transport process. April and May, the time of shift to a summer wind pattern in the MAB, consistently provide a sufficient number of southerly events to transport larvae spawned late in the season northward toward Chesapeake Bay.

Year-class strength is hypothesized to be dependent on the number of southerly events occurring prior to the wind shift. Average year classes would rely totally on the wind-induced transport during April/May, very poor year classes would result when there was a reduced number of southerly events during April/May, and dominant year classes would then be dependent on the number of southerly events occurring from January through March. Analysis of the four-day southerly wind events occurring during this three month period detected a significant difference ($F = 2.55$; df = 9,18; $P<0.05$) between years. Results from the total number of southerly wind events was not conclusive ($F = 1.92$; df = 9,18; $P = 0.114$), but still reflected a difference between years.

Analysis of monthly or seasonally averaged winds indicates that winter is not favorable for onshore transport south of Cape Hatteras (Yoder 1983). These time scales conceal short periods of wind variability which are important for larval fish transport. Transport across the southeastern U.S. shelf in winter can be explained by 'event' scale wind reversals which are most numerous in the outer regions (Yoder 1983). The most favorable shelf current regime for shoreward transport is hypothesized to be in the mid-layer during winter (Miller et al. 1984; Miller et al. 1985). A three-layer winter offshore/onshore transport regime, combined with vertical migration of larvae, may keep the fall/winter spawned larvae offshore and delay entrance to North Carolina estuaries during winter (Miller et al. 1984). Perhaps there is a similar mechanism which bypasses or only partially uses this physical regime and results in transport around Cape Hatteras and northward to Chesapeake Bay. This would be consistent with 57–82 day old fish (Siegfried 1989) entering a Chesapeake Bay estuary. Alternatively, since the water column north of Cape Hatteras is unstratified at this time of year (Beardsley et al. 1976), reducing the effect of Ekman transport on the upper water column, the transport mechanism may be less complex. For 90 days, spot larvae are buffeted both north and south by winds and currents but the additive product of pulses of southerly winds cause a resultant northward movement.

Information on distribution of spot larvae during winter and early spring in the MAB is limited (Berrien et al. 1978; Morse et al. 1987; M. Fahay, NMFS/NEFC, Highlands, NJ 07732, pers. commun. Nov. 1988). Distribution of spot larvae (Fig. 5) in November–December was concentrated south of Cape Hatteras and spread northward to Oregon Inlet. Larvae collected during February were primarily south of Oregon Inlet with highest densities found near Cape Hatteras. By March, the larvae were widely distributed from south of Cape Lookout to the area off False Cape, VA, south of the Chesapeake Bay mouth. Distribution continued to progress northward during April when larvae were found north of the mouth of Chesapeake Bay. During May, the regional distribution was further condensed with almost all larvae found north of False Cape.

The extent of distribution varied from year to year, but several patterns can be seen. Distribution of larvae spread northward to Chesapeake Bay over time and most larvae were captured inshore where waters are prone to wind-induced current reversals. Mean size of larvae increased from offshore to inshore and with distance northward, suggesting a spawning site near or south of Cape Hatteras on the outer shelf. The range of larval sizes found each month further emphasized the protracted spawning period.

Distribution of larvae, coupled with information on size and age, has been used in the South Atlantic Bight to infer time and area of spawning (Lewis and Judy 1983; Warlen and Chester 1985). From Cape Hatteras southward, the highest larval abundance in winter (November–March) is on the outer shelf in depths of 40–200 m (Lewis and Judy 1983; Yoder 1983; Warlen and Chester 1985). Concurrently, surface temperatures there are warmer and more favorable for spawning and larval survival (Yoder 1983).

Pelagic larvae are unable to regulate their environment, but they may moderate the effects through an appropriate behavioral response to reliable environmental signals (Leggett 1985). Microscale migrations of larvae of several species have been shown to influence their association with beneficial current regimes, resulting in transport into estuarine nursery grounds (Leggett 1985; Miller et al. 1985). Therefore, it is possible that spring reversals of wind patterns north of Cape Hatteras could act as an environmental signal to which spot larvae respond, resulting in northward transport to Chesapeake Bay. However, early larval survival is highly variable when dependent upon such large-scale meteorological events (Leggett et al. 1984). Such

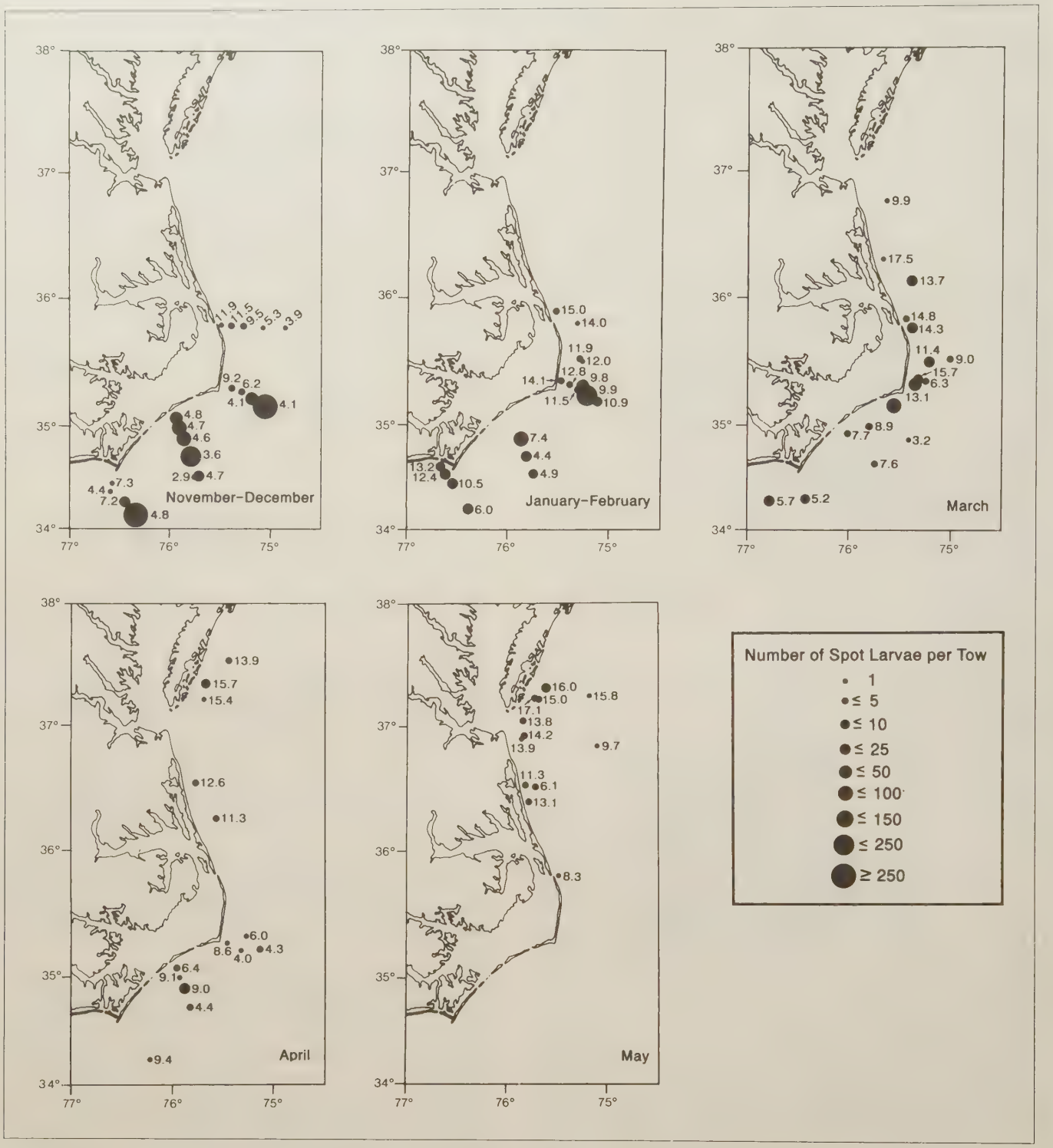

Figure 5

Aggregate seasonal distribution and abundance of spot larvae from the RV *Dolphin* cruises (1965–1966) (Berrien et al. 1978) and NMFS/NEFC surveys (1977–1986) (M. Fahay, NMFS/NEFC, November 1988). Numbers indicate mean size of larvae (mm).

variable recruitment of spot is common in Chesapeake Bay and Delaware Bay (Thomas 1978).

Data on juvenile spot recruitment in Virginia are not available from the same time period as the larval collections, but they are available from recent samples collected from 1986 to 1988. In 1987, spot first appeared during the second April collection period, 20–23 April, recruitment peaking in May and continuing through June (Fig. 6). The

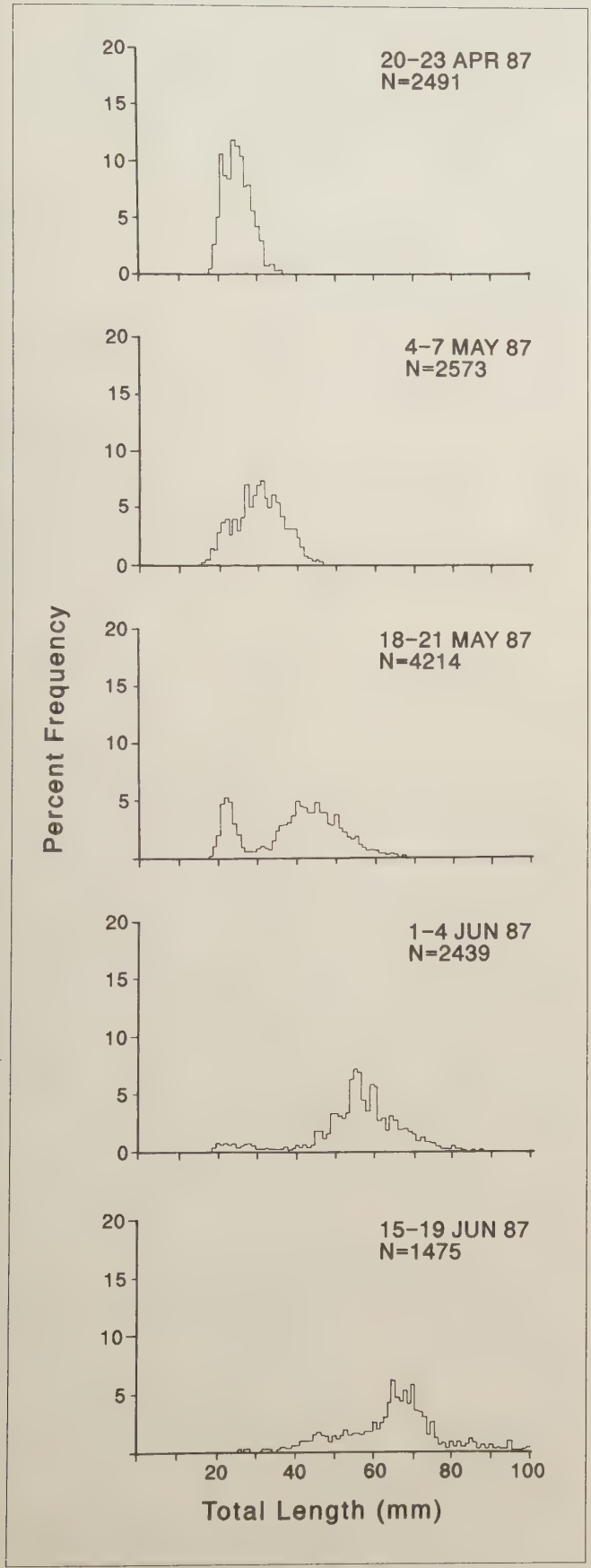

Figure 6

1987 bimonthly sampling. Length/frequency histograms of newly recruited spot aggregated over five sites in Chesapeake Bay and on the eastern shore of Virginia (from top to bottom: Wachapreague, Sand Shoal, Fisherman's Island, Occohannock Creek, and York River).

trend of peak recruitment in May and June was also seen in 1988 collections, but spot appeared in Chesapeake Bay during March (Fig. 7), a month earlier than in 1987. The March/April appearance of recruits between 13 and 41 mm TL is in agreement with most other reports of spot entrance to Chesapeake Bay (Table 1).

Evidence of a protracted spawning season is seen with the presence of new recruits (10–25 mm TL) in all collections (Figs. 6 and 7). Episodes of southerly winds in 1987 and 1988 occurred prior to the initial appearance of spot within Chesapeake Bay and prior to the appearance of each successive cohort (Fig. 3). The earlier arrival of spot in March 1988 could be related to the number (12) of southerly wind events in February as opposed to 1987 when there were no southerly events in February (Fig. 4) and spot did not appear until late April.

Based on the growth rates of Warlen and Chester (1985) and Siegfried (1989), spot entering Chesapeake Bay in 1987 and 1988 were spawned between January and April. At that time of year, the only bottom water warmer than 17°C was just off Cape Hatteras (Fig. 2), 250 km south of Chesapeake Bay.

It is not impossible for fish larvae to be transported in excess of 250 km to reach nursery grounds. Larvae of the American eel (*Anguilla rostrata*) and bluefish (*Pomatomus saltatrix*) are also transported northward along the Atlantic coast before entering estuaries. However, unlike spot, it is thought that transport of these species is dependent upon the Gulf Stream (Kendall and Walford 1979; Kleckner and McCleave 1982). The apparent dependence of pelagic spawners on "normal" oceanographic drift conditions suggests that anomalies in these patterns could result in variation in recruitment success (Norcross and Shaw 1984). The suggested "normal" condition affecting spot recruitment to Chesapeake Bay is episodes of southerly reversals in spring wind patterns. The timing of these reversals is hypothesized to cause observed anomalous variations in spot recruitment abundance.

The hypothesis that wind events are responsible for a portion of the interannual variability in spot recruitment suggests the need for investigation of the offshore larval distribution coupled with the physical dynamics of the system. Circulation patterns over the MAB continental shelf and around Cape Hatteras are complex, and transport processes may also be related to the amount of estuarine discharge, tidal influence, and stratification of the water column. Current meter data for the MAB south of Chesa-

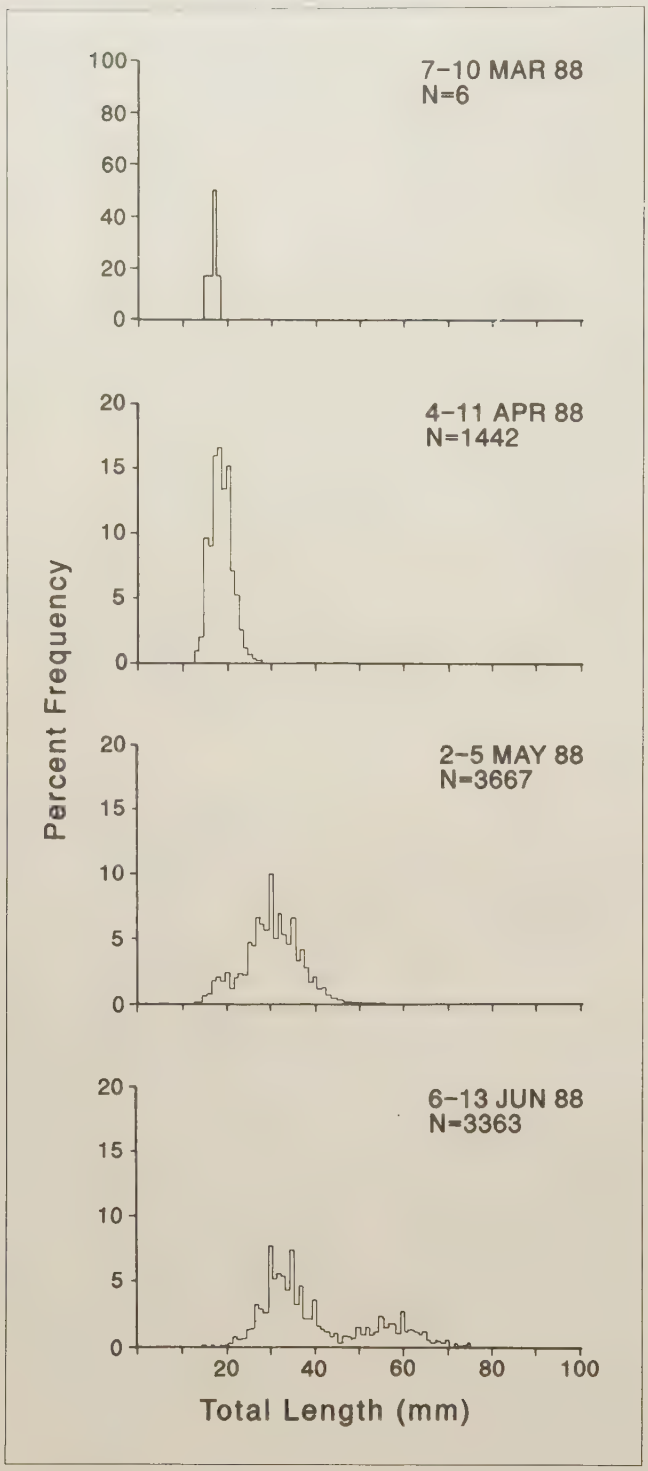

Figure 7
1988 monthly sampling. Length/frequency histograms of newly recruited spot aggregated over five sites in Chesapeake Bay and on the eastern shore of Virginia (from top to bottom: Wachapreague, Sand Shoal, Fisherman's Island, Occohannock Creek, and York River).

peake Bay are needed to verify inferences of water movement in conjunction with southerly wind events. Computer simulations of the shelf currents would aid in identifying physical factors that have the greatest effect on recruitment variation. This effect would be further modified by the vertical distribution of spot larvae, though this distribution is currently unknown. Discrete depth collections are therefore needed to determine depth distribution of spot larvae and associated changes which may occur as larvae develop. Field studies are needed to verify spot spawning sites and to collect concomitant physical data. The possibility exists that fish recruiting to areas north of Cape Hatteras are spawned at a later date than those recruiting to more southern estuaries. Aging of larvae, based on daily otolith increments, would yield information on spawning time, duration of transport, and growth rates during the larval phase. Sampling of new recruits on a time scale finer than the monthly and bimonthly data presented here is necessary to adequately test the hypothesized relationship with southerly wind events.

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Ichthyoplankton Assemblages Sampled by Night Lighting in Nearshore Habitats of Southwestern Puerto Rico

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ABSTRACT

Larval fishes were sampled in four nearshore habitats: coral reef, seagrass bed, mangrove lagoon, and mangrove prop roots in southwestern Puerto Rico. A lift net with attached night light was employed to determine seasonal abundance and species composition of the nearshore ichthyoplankton assemblage. Coral reef and seagrass bed habitats usually possessed the greatest abundance and species richness of larval fishes. Few early stages of larval fishes were collected in mangrove habitats suggesting that they were not nursery areas. The abundance of larval fishes in the open water area of the lagoon was not significantly different from the prop root habitat. Although all habitats were within close proximity (ca. 2 km), there were different patterns in abundance between the coral reef/seagrass bed and mangrove habitats. Based on low abundance of larval fishes and few species captured, the mangroves cannot be considered an important spawning or nursery area for larval fishes in southwestern Puerto Rico.

Introduction

Larval fishes in nearshore tropical environments have not been thoroughly studied because of the difficulty in using standard ichthyoplankton sampling gear in these areas. A major problem encountered when sampling tropical nearshore waters with an active gear, such as a towed net, is navigation among shallow reef areas. Sampling at night amplifies navigational problems, but may be particularly important in nearshore areas where larval fishes may aggregate near bottom or visually avoid towed nets during the day (Powles 1977; Thayer et al. 1983). Thus, most tropical ichthyoplankton studies have been concentrated in oceanic waters where large vessels can operate (Ahlstrom 1971, 1972; Powles 1975; Leis and Miller 1976; Richards 1984). Few studies have examined ichthyoplankton around mangroves (Wyatt 1982; Flores-Coto et al. 1983; Collins and Finucane 1984; Little et al. 1988; Powell et al. 1989) even though these areas are considered major fish nurseries (Heald and Odum 1970).

This study addresses the hypothesis that mangrove areas are spawning or larval nursery areas for fishes in southwestern Puerto Rico. We employed a lift net with attached night light to reduce the problem of sampling with towed nets in coral reef and mangrove habitats.

Materials and Methods

Sampling Area

The study area was located on the southwestern coast of Puerto Rico, the most easterly large island in the Greater Antilles (Fig. 1). The coast is fringed by relatively undisturbed red mangrove forests (*Rhizophora mangle*) and nearshore waters are dotted with red mangrove cays. Many well-developed coral reefs are also found in the area. This portion of Puerto Rico has a dry climate with a total rainfall of 695 mm for 1988. There are no rivers and little freshwater runoff; hence water quality is good. Larval fishes were sampled in four nearshore habitats: mangrove prop root, mangrove lagoon, seagrass bed, and coral reef.

The mangrove prop root habitat included the prop root system adjacent mangrove produced muddy bottom areas (Dennis, in press). Soft mud bottom abutted the mangroves and average water depth for prop-root stations averaged 1.2 m. Four sampling stations were selected here.

A small lagoon surrounded by red mangroves served as the mangrove lagoon habitat and was the primary mangrove habitat sampling site (Fig. 1). The lagoon station

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Figure 1

Map of sampling area in southwestern Puerto Rico. M is the primary mangrove sampling site (4 prop-root stations and one lagoon station). BA and BB are additional mangrove lagoons. SG is the seagrass bed station and CR is the coral reef station.

was over soft mud and had a depth of 2 m. One lagoon station was established near the center of the east entrance to the lagoon. Two additional mangrove lagoons to the west of the primary lagoon were also sampled (Fig. 1). They also had a soft mud bottom and an average depth of 1 m.

A seagrass bed station (Fig. 1) was selected off Isla Cueva on a shallow platform primarily covered with *Thalassia testudinum* and some small gorgonians and coral patches. Water depth at this site was 1.5 m.

A coral reef station was located on a fringing reef off the leeward end of a mangrove cay (Fig. 1). The reef was dominated by *Acropora palmata* and *Millepora* spp. The sample site was directly over coral in a water depth of 1.7 m. Adjacent to the reef the bottom was covered with seagrass.

Sampling Methods

We used a lift-net with a night light as a sampling device, composed of a floating platform housing a circular 12-volt sealed-beam automobile headlight bulb (Fig. 2). A standard 50-cm diameter by 165-cm long conical plankton net of 500-micron mesh was attached to the platform by four guide ropes. Power for the light was supplied by a 12-volt marine battery aboard a 6-m fiber-glass support boat.

Sampling consisted of lowering the plankton net to a depth of one meter or less depending on bottom depth, then turning on the light for 10 minutes. The net was then rapidly hoisted to the surface by hand while the light was still on and it sampled fish in the water column between the net and light source. Sampling characteristics of this device are discussed in detail (D. Goulet et al. 1988).

Three replicates were taken at each station during each sampling period. Coral reef and seagrass bed stations were sampled sequentially with a 10 minute no-light period between replicates; mangrove stations were alternately sampled. The order of station sampling was randomly selected and all samples taken within one day of the new moon from 2000 to 0100 hours.

Monthly samples were collected at the four prop-root mangrove stations in August, September, and October 1987; at one of these stations from September 1987 to February 1989; and at the mangrove lagoon station from October 1987 to February 1989. Two additional mangrove lagoons (Fig. 1) were sampled in February 1989. No samples were taken at the mangrove stations in November 1988. Seagrass bed and coral reef stations were sampled from March 1988 to February 1989. Because of inclement weather and gear failure, samples were missed in August 1988 at the seagrass bed station and in August and September 1988 at the coral reef station. No samples were

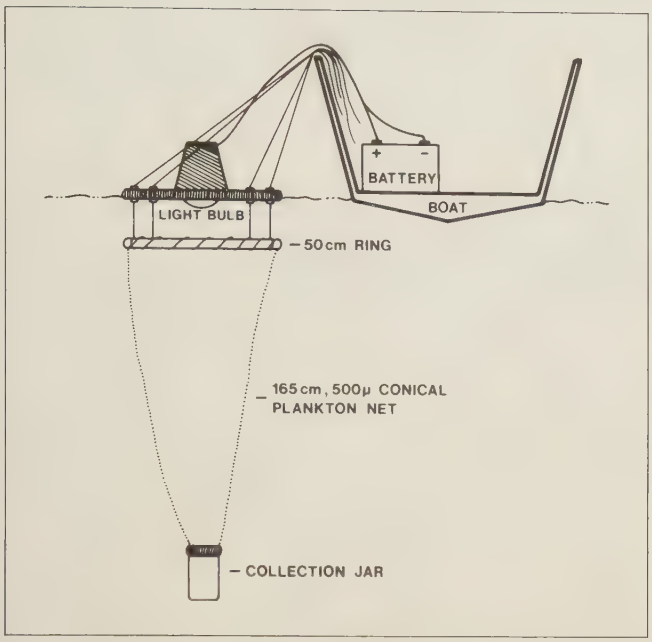

Figure 2
Lift-net sampling device with night light.

taken in January 1989. Water temperature, salinity, and dissolved oxygen were measured at 0.3 m below the surface at each station.

Samples were initially preserved in 10% formalin and transferred to 5% formalin within one week. After sorting, identification, and measurement, the fishes were stored in 70% ethanol. All fishes were identified to the lowest taxon possible. A taxon was defined as a distinct life-history stage of a species. Life-history stages included: preflexion larvae (before notochord flexion), postflexion larvae (after notochord flexion and including flexion larvae), and juveniles (fish with a full complement of adult fin ray counts) (after Leis and Rennis 1983).

We considered mangroves to be spawning areas for fishes if early preflexion larvae were abundant in that habitat. Also, if mangroves are larval nursery areas, then later stage (postflexion) larvae should be abundant there.

Analysis

Two-way ANOVA analyses were carried out on log transformed $(x + 1)$ abundance data for total number of taxa, total number of larvae, total number of non-dwarf herring (*Jenkinsia* spp.) larvae, and the four most abundant taxa, dwarf herring, sardine (*Harengula* spp.), anchovies (*Anchoa* sp.), and bonefish (*Albula vulpes*) to test for differences in abundance among habitats and months. Only the eight months when all habitats were sampled were used in this ANOVA. A two-way ANOVA among the four primary mangrove prop-root stations and months was used to test for significant differences in number of larvae among locations within a mangrove lagoon. Samples were taken during three consecutive months (August–October 1987) for this analysis. Two additional mangrove lagoons (Fig. 1) were compared to Lagoon M during February 1989 with a two-way ANOVA by habitat (lagoon and prop roots) and location (three mangrove lagoons) to test for differences among lagoons. Tukey's HSD test was used to determine which levels of a factor were significant (Sokal and Rohlf 1981).

Additional comparisons of larval abundance were made among habitats (summed over all sampling periods) with a chi-square test assuming larval abundance was proportional to sampling effort.

Similarity among habitats was measured by the percent similarity formula, $PS = 1 - 0.5 \sum |p_{x,i} p_{y,i}|$, where $p_{x,i}$ = proportion of taxa i in habitat x and $p_{y,i}$ = proportion of taxa i in habitat y based on abundance over all sampling periods (Kohn and Riggs 1982). Unweighted pair-group arithmetic average (UPGMA) clustering was used to create the similarity dendrogram (Sneath and Sokal 1973).

Results

Habitats had significantly different patterns of larval fish abundance (Figs. 3 and 4). In all cases there was a significant interaction between habitats and months which indicated that habitats had different trends in larval fish abundance over time (F-test, habitat by month interaction term, $P<0.01$). The mangrove lagoon and prop-root stations differed from coral reef and seagrass bed stations in their patterns of abundance. Larval fish were most abundant at seagrass and coral reef stations from February to April while larvae were most abundant in the mangroves in July (Fig. 3). There was a greater number of taxa at seagrass bed and coral reef stations from December to April, but there was little difference among the four habitats from June to October.

Seasonal patterns of abundance differed among habitats for the most abundant taxa (Fig. 4). From March to April, bonefish larvae were abundant at the coral reef station, but over the whole sampling period they were more commonly collected at the mangrove prop-root station.

Dwarf herring were the most abundant larvae taken, and were primarily collected from seagrass bed and coral reef stations (Fig. 4). Patterns in abundance of dwarf herring larvae (preflexion and postflexion) were similar over time at the coral reef station with a major abundance peak in February 1989 and smaller peaks in May 1988 and October 1988 (Fig. 4). The seagrass bed station differed from the coral reef station in lacking an abundance peak in May 1988 and having a peak in March 1988 (Fig. 4).

The sardine was most commonly collected at mangrove and seagrass bed stations, but few were taken at the coral

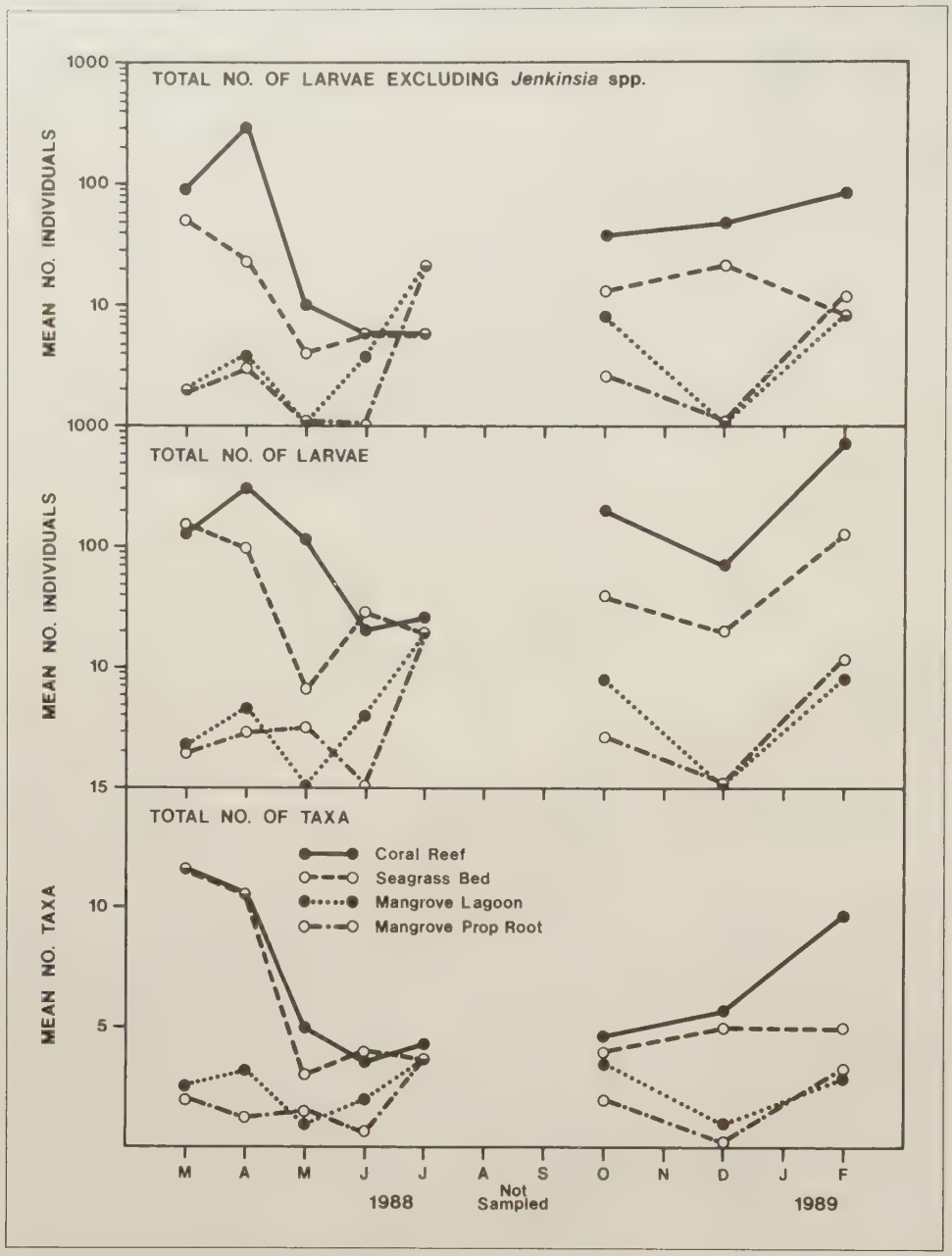

Figure 3
Monthly trends in arithmetic mean number of larvae excluding *Jenkinsia* spp., number of taxa, and number of larvae by habitat.

reef station. The anchovy was primarily collected from mangrove and seagrass bed stations with a major abundance peak in July at mangrove stations and another smaller peak between September and October at seagrass bed and mangrove lagoon stations.

The coral reef station had more preflexion and postflexion larvae than other stations (Chi-square test, $P<0.01$, in both cases). Bonefish (*Albula vulpes*), sea bream (*Archosargus rhomboidalis*), preflexion and postflexion dwarf herring (*Jenkinsia* spp.), preflexion and postflexion silversides (Atherinidae), Clinidae species 1 and 2, and unidentified preflexion larvae, were also significantly more abundant at this station (Table 1) (Chi-square test, $P<0.01$ in all cases). The coral reef station was most similar to the seagrass bed station and very dissimilar to mangrove stations (Fig. 5).

The seagrass bed station had significantly more taxa, preflexion larvae, postflexion larvae, and juveniles than mangrove stations (Table 1) (Chi-square test, $P<0.01$). Four taxa were most common here: Gobiidae species 2, dwarf herring juveniles, and sardine postflexion larvae and juveniles. Also, dwarf herring postflexion larvae were significantly more abundant at this station than at mangrove stations (Chi-square test, $P<0.01$). The seagrass bed station had an intermediate assemblage of larval fishes relative to coral reef and mangroves, but was much more

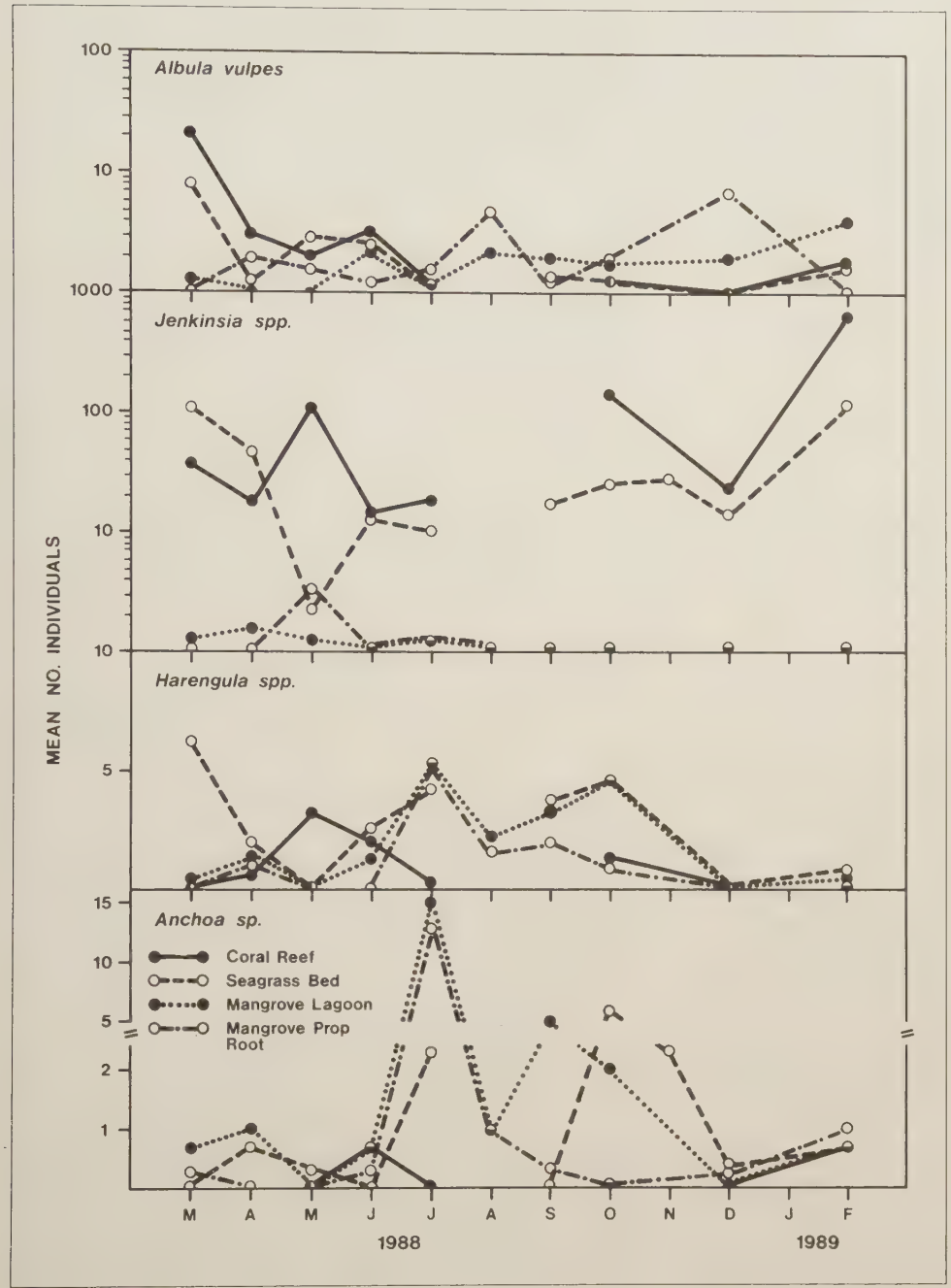

Figure 4
Monthly trends in arithmetic mean number of *Albula vulpes*, *Jenkinsia* spp., *Harengula* spp., and *Anchoa* sp. by habitat.

similar to the coral reef station than the mangrove stations (Fig. 5).

Mangrove stations, in general, had fewer taxa and number of larvae than coral reef and seagrass bed stations (Table 1). The mangrove lagoon had more preflexion larvae and postflexion sardine larvae than the prop-root station (Chi-square test, $P<0.01$ in both cases). Only two taxa were more abundant at the prop-root station, bonefish and gerreid larvae, and the latter was significantly more abundant at the prop-root station than at any other station (Chi-square test, $P<0.01$). Mangrove stations were very similar to each other and next most similar to the seagrass bed station (Fig. 5).

Examination of larval fish abundance within lagoon M at four prop-root stations over a three month period indicated similar trends in larval abundance among stations (F-test, station by month interaction, $P = 0.273$). Months were significantly different in larval fish abundance (F-test, $P = 0.012$), but there was only a marginally significant difference among stations (F-test, $P = 0.041$).

Comparison of larval fish abundance among three mangrove lagoons indicated no interaction between habitats

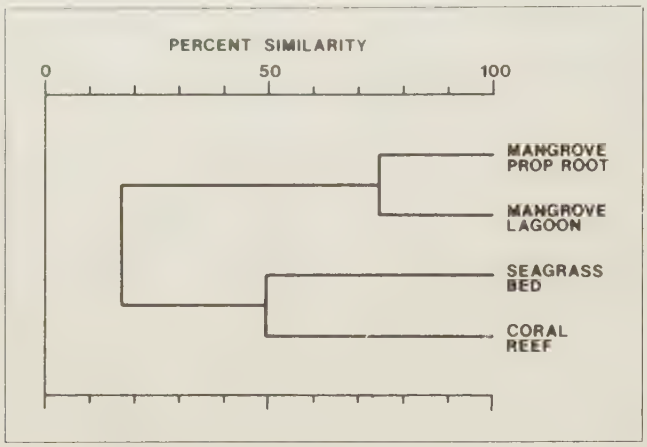

Figure 5
Similarity among habitats based on taxon abundance over all sampling periods. Dendrogram formed by UPGMA method on percent similarity (PS).

and locations (F-test, $P = 0.553$) and no significant difference between habitats (F-test, $P = 0.629$). There was a significant difference in larval fish abundance among lagoons with the primary sampling lagoon (M) having significantly more larvae than the other two (F-test, $P = 0.012$, Tukey's HSD test, Sokal and Rohlf 1981).

Salinity was high (34–37 ppt) at all stations, even during the rainy season. Water temperature during the study ranged from a low of 26.0°C in January–February to a high of 30.5°C in July, but differed less than 1°C among stations during any sampling period. Dissolved oxygen usually ranged from 5 to 7 ppm, but on one occasion measured 2.5 ppm near bottom at a mangrove prop-root station. There was little variation in environmental parameters among stations within any sampling period.

Discussion

Almost any active method of collecting ichthyoplankton in waters with obstructions will result in sampling difficulties. One solution to this problem is the use of a passive aggregating device, such as light. Its application has been primarily relegated to a qualitative, ancillary role in the past. Using light as a quantitative method of sampling can been criticized on two main points: volume sampled is unknown and species selectivity bias.

Volume sampled is dependent on water clarity and current speed. Theoretically, more turbid water should result in fewer larvae attracted owing to a smaller area of light influence. Greater current speed should (up to the point where larvae can no longer maintain their position) result in more larvae passing within the sphere of light influence and in potentially being retained in the area for collection. Current velocity in the nearshore environment is primarily a result of daytime wind-driven circulation in locations, such as the Caribbean, where there is a limited tidal range (ca. 0.5 m). Nighttime, usually a period of low wind, further reduces the influence of current speed on volume sampled. In this study we attempted to control these factors by sampling in areas of similar high water clarity and keeping the duration of sampling short (10 minutes).

Light is selective both for taxonomic composition and size. Though taxon selectivity is not well documented, it is known that different stages of some fish species react differently to light (Bulkowski and Meade 1983). Still, there is a tremendous range of taxa collected by light methods (Doherty 1987) and this same bias is known to occur in towed gears (Thayer et al. 1983). In this study forty-five taxa represented by 7342 larvae were taken.

Size selectivity may be species specific and biased toward either smaller or larger size groups in active gears depending on gear type. Larger larvae are usually less well sampled because they avoid the net (Thayer et al. 1983; Gregory and Powles 1988). Methods using light usually catch more later-stage larvae (presettlement) and juveniles than towed-net gears (this study; Doherty 1987) making them potentially complementary methods for sampling larval fishes.

Although the four habitats sampled were only about 2 km apart, they exhibited different patterns in larval fish abundance. Abundance peaked from February to April at coral reef and seagrass bed stations, but peaked in July and August at mangrove stations when densities at coral reef and seagrass bed stations were lowest. The different patterns in these two nearby areas seemed to contradict the idea of passive dispersal of preflexion larvae within the nearshore environment. Normal wind-driven circulation from the southeast should push water (and preflexion larvae) from nearshore reefs and seagrass beds into mangrove areas. This circulation alone would increase the abundance of preflexion larvae in the mangroves. But preflexion dwarf herring larvae were never collected in mangroves, though juveniles and adults commonly occur there. Even between the coral reef and seagrass bed stations there was little coherence in peaks of abundance for preflexion dwarf herring larvae. This species, instead, makes use of epibenthic and benthic areas and therefore may not be subjected to passive transport by currents (Powles 1977; pers. obs.).

The mangrove prop-root habitat had a low density of larval fish, as did the "open water" lagoon station. Yet larval gerreids, bonefish, and sardine made use of the mangrove habitat. The generally low density of larval fishes in mangrove habitats did not support the hypothesis that these areas are nurseries for larval fishes at least in southwestern Puerto Rico. Several studies support our findings. In the Florida Everglades, there were fewer taxa and larvae taken by towed net in mangrove estuaries than in nearshore areas (Collins and Finucane 1984). Highest diver-

Table 1

Number of fishes by taxa collected by night lighting in four nearshore habitats off southwestern Puerto Rico. Mangrove habitats include only the primary mangrove sampling site (see Fig. 1). Life-history stages are PR: preflexion, PO: postflexion, and J: juvenile.

Taxa	Stage	Habitat				Total
		Coral Reef	Seagrass Bed	Mangrove Lagoon	Mangrove Prop Root	
ALBULIDAE *Albula vulpes*	PO	90	51	36	101	278
APOGONIDAE	PO	—	1	—	—	1
ATHERINIDAE	PR	393	35	15	2	445
	PO	29	3	—	1	33
CARANGIDAE	PO	1	—	—	—	1
Oligoplites saurus	J	—	—	3	8	11
Trachinotus sp.	PO	—	—	—	1	1
CLINIDAE Species 1	PO	22	4	—	—	26
Species 2	PO	58	14	—	—	72
CLUPEIDAE *Harengula* spp.	PO	27	90	91	65	273
	J	24	129	106	112	371
Jenkinsia spp.	PR	2216	115	—	—	2331
	PO	1106	1043	8	3	2160
	J	189	324	3	5	521
Opisthonema oglinum	PO	—	—	6	—	6
	J	—	—	2	—	2
DACTYLOSCOPIDAE	PO	1	—	—	—	1
ELOPIDAE *Elops saurus*	PO	1	—	—	—	1
ENGRAULIDAE *Anchoa* sp.	PR	3	2	1	—	6
	PO	2	47	67	54	170
	J	2	7	4	10	23
GERREIDAE	PO	3	5	3	25	36
GOBEISOCIDAE Species 1	PO	6	—	—	—	6
Species 2	PO	13	2	—	—	15
GOBIIDAE Species 1	PO	4	12	—	—	16
Species 2	PR	2	10	—	1	13
	PO	10	71	1	3	85
Species 3	PO	1	3	—	—	4
Species 4	PO	—	1	1	2	4
Species 5	PO	—	1	—	—	1
LUTJANIDAE	PO	3	—	—	1	4
OPHIDIIDAE	PO	2	1	—	—	3
HAEMULIDAE	PO	8	4	—	—	12
MUGILIDAE *Mugil* sp.	PO	1	1	6	2	10
POMACENTRIDAE	PO	—	—	1	—	1
SCARIDAE	PO	2	2	—	—	4
SCORPAENIDAE	PO	1	—	—	—	1
SERRANIDAE *Epinephelus itajara*	PO	—	—	3	—	3
Hypoplectrus sp.	PO	—	1	—	—	1
SPARIDAE *Archosargus rhomboidalis*	PO	101	24	11	21	157
SPHYRAENIDAE *Sphyraena barracuda*	J	—	—	2	2	4
SYNGNATHIDAE	PO	7	1	—	—	8
SYNODONTIDAE *Synodus* sp.	PO	2	—	—	—	2
Undetermined larvae	PR	1000	16	8	1	1025
	PO	3	1	—	—	4
Total No. of Taxa		34	31	21	20	45
Total No. of Larvae		5118	1561	258	405	7342
Preflexion		3614	178	24	4	3820
Postflexion		1504	1383	234	279	3400
Juveniles		215	460	120	137	932
No. of Samples		27	30	45	51	127

sity and abundance of larval fishes was also found at nonestuarine stations by Powell et al. (1989) in Florida Bay, where spawning (based on preflexion larval abundance) occurred in intermediate to high salinities. Flores-Coto et al. (1983) found most larvae in Tamiahua Lagoon (western Gulf of Mexico) to have originated there and few larvae entered the lagoon from nearshore waters. Within Tamiahua Lagoon the greatest abundance of larvae was in the center of the lagoon away from shoreline habitats. The number of fish eggs decreased with increasing estuarine conditions in mangrove areas of Kenya (Little et al. 1988) and India (Krishnamurthy and Jeyaseelan 1981). There was also a gradient from high to low abundance of larval fish from the mouth to upper reaches of a mangrove creek in Kenya (Little et al. 1988).

Patterns of larval fish abundance in tropical nearshore island habitats may be different from tropical or temperate estuaries where migration into the estuaries from nearshore waters is more typical (Weinstein 1979; Weinstein et al. 1980; Shaw et al. 1988). The predominance of reef-associated species and high salinity conditions in tropical nearshore island habitats may account for a limited coupling with the shelf fish assemblage.

Haemulid and lutjanid larvae were noticeably absent from our collection, even though they comprised about 55% of juvenile fishes in mangroves of this area (Dennis, in press). It is possible that these taxa were not attracted to light at the stage they entered the prop-root habitat or settled in other nearby habitats and migrated to the prop roots. In Florida Bay, few snapper larvae were collected in shallow water areas, but preflexion larvae were found at the shelf edge near coral reefs (Powell et al. 1989).

It is also possible that many taxa may recruit to nearshore habitats in short duration periods (ca. 1–3 days) which are easily missed by monthly sampling (Doherty 1987). We observed this phenomenon in September 1988 when three jewfish (*Epinephelus itajara*) larvae were collected at the mangrove lagoon station. The following night we sampled at the marine station dock on Isla Magueyes (a mangrove-fringed island about 3.5 km east of lagoon M) (Fig. 1) and collected three additional jewfish larvae. The third night no jewfish larvae were collected. Though the complete duration of the jewfish recruitment event is not known, probably only fortuitous sample timing leads to capture of this and possibly other species.

Smith et al. (1987) described the nearshore assemblage of fish larvae as differing from that found offshore by being composed of morphologically unspecialized forms that may spend their complete larval phase nearshore. The nearshore larval fish assemblage collected off southwestern Puerto Rico fits this description as it was composed of common shallow-water fish families with few specialized larval forms (e.g., bonefish *leptocephali*, jewfish larvae). Without synoptic sampling across the shelf we are unable to estimate what proportion of the larval fish assemblage might have originated and remained in the nearshore environment, but several taxa, such as bonefish, sardine, jewfish, and lutjanids were collected only at late development stages, an incident which suggests recruitment from outside the nearshore environment. Cross-shelf sampling will be needed before the source of some taxa can be determined.

The lack of many larval fish taxa in mangroves might be attributed to the numerous piscivore predators that reside in mangrove prop roots (Dennis, in press) and to periodically poor environmental conditions. Sluggish water movement and high biological oxygen demand can result in occasionally low oxygen conditions in the mangroves. One incident of depressed dissolved oxygen level (2.5 ppm) was measured near bottom at night in the mangrove prop roots. The effect of low oxygen on ichthyoplankton should be ascertained before there is further judgment on the quality of mangrove areas as nursery grounds for larval fishes.

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Microhabitat and Diet Segregation among Coexisting Young-of-Year Sunfishes (Centrarchidae)

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ABSTRACT

Young-of-year (yoy) sunfishes (*Lepomis* spp.) often remain in vegetated habitats in order to avoid predators and thereby limit opportunities to partition resources. Minnow traps were used to collect yoy of five species of sunfishes to determine their diet and use of microhabitats (type of vegetation, water depth, and substrate type) in Lake Rush, Oklahoma. The relative importance of each of these niche dimensions in separating species varied between years (1980 and 1981) in response to changes in the abundance and composition of aquatic macrophytes. In 1980 the type of vegetation was important in separating nine of ten species pairs, but only three pairs had low overlap along this dimension in 1981. Use of water depth effectively separated warmouth (*L. gulosus*) from redear sunfish (*L. microlophus*), longear sunfish (*L. megalotis*), and green sunfish (*L. cyanellus*) in 1980; but depth distributions of redear sunfish, longear sunfish, and warmouth were more similar in 1981. Longear sunfish was the only species that used mainly coarse substrates in both years. Although estimates of species segregation by diet may be conservative, dietary differences among five species pairs in 1980, and four pairs in 1981, were substantial. Niche complementarity was evident in both years. Bluegills (*L. macrochirus*) and redear sunfish had nearly total overlap for substrate type but overlapped little for use of vegetation in 1980 and diet in 1981.

Introduction

Resource partitioning among coexisting fish species in aquatic communities has been widely studied (Ross 1986). Such differential use of resources may be due to many factors. Among sunfishes (*Lepomis* spp.), adults and subadults clearly partition resources (Werner et al. 1977; Laughlin and Werner 1980), but there is little evidence that young-of-year (yoy) of these species do so. In fact, Laughlin and Werner (1980) and Mittelbach (1984) found that young of all species of sunfish were confined to vegetation. They suggested that vegetation provided a refuge from predators, and that confinement to vegetation could increase the intensity of interspecific interactions. Because it is always profitable for species to avoid competition when possible (Pianka 1976), overt competition is rarely observed in established communities; instead, postcompetitive relationships, whereby coexisting species divide resources, are more evident than instances of apparent competition. The common coexistence of sunfishes in North American waters suggests that these species, including their young, may have resolved conflicts in resource exploitation.

Five species of yoy sunfishes often were collected from Lake Rush, southwestern Oklahoma, in the same seine haul over a seemingly homogeneous area: bluegill (*L. macrochirus*); redear sunfish (*L. microlophus*); longear sunfish (*L. megalotis*); warmouth (*L. gulosus*); and green sunfish (*L. cyanellus*). A cursory examination of the stomach contents from several individuals of each species suggested that they ate similar foods. Growth of centrarchids during the first year of life in Lake Rush is slow; mean total lengths of yoy sunfishes collected in late October varied from 34 mm for bluegills to 43 mm for longear sunfish (Layzer 1982). Since these sizes are below average for Oklahoma (Mense 1976), it could be inferred that some resource (presumably food) was limiting fish production. If so, resources might be partitioned to allow continued coexistence. We here attempt to resolve the apparent contra-

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diction between our preliminary observations of similar patterns of resource use by sympatric yoy sunfishes and the expected partitioning of resources under an assumed regime of a limited resource.

Study Area

Lake Rush, located in the Wichita Mountains National Wildlife Refuge in southwest Oklahoma, is a 20.9-ha impoundment on Blue Beaver Creek. Maximum depth is 10 m and average depth is 4.8 m. Typically, flow from Blue Beaver Creek and other tributaries stop by early to mid-July. Lake Rush becomes thermally stratified by mid-June, with near anoxic conditions in the hypolimnion (depth 3 m). Secchi disc depth averaged 1.45 ± 0.05 m during the summers of 1979 and 1980. The elongated basin of the impoundment lies along an east-west axis; littoral areas are primarily along the northern and southern shorelines. The southern shoreline has a steeply sloping bottom; a firm, heterogeneous substratum consisting of a mixture of particles ranging from coarse sand to large boulders, and a few small isolated patches of water milfoil (*Myriophyllum* sp.). The northern side has a gently sloping bottom with a sandy-silt substratum overlain with fine organic detritus and dense stands of aquatic macrophytes.

The distribution and composition of the submergent vegetation changed markedly during the study as a result of an application of 2,4-D herbicide crystals by refuge personnel in April 1981. In 1980 strikingly apparent zones of the plant community were each dominated by a single species. The emergent zone was 5 to 10 m wide and extended from the shoreline out to a depth of about 75 cm. This area was densely populated by spikerush (*Eleocharis* sp.). Unlike lakes with stable water levels, the emergent zone was bordered by a submergent zone 3 to 5 m wide out to a depth of 110 cm, dominated by muskgrass (*Chara* sp.). This zone was apparently created by low lake levels which occurred from late summer to early spring during most years. Continuous with this zone and out to a depth of 1.8 to 2.5 m was a 30 to 60 m wide band of water milfoil interrupted by isolated patches of pondweed (*Potamogeton* spp.); American lotus (*Nelumbo lutea*); and coontail (*Ceratophyllum demersum*). The outer band of vegetation, which was more irregular, was composed entirely of coontail to a depth of 2.5 to 2.8 m. These water depths and associated plant distributions existed only during portions of 1980 when the lake was full. Since the source of water is primarily surface runoff, the lake level varies seasonally. In 1979 and 1980, levels were maximum in the spring and decreased throughout the summer, gradually exposing the emergent zone and most of the muskgrass by early fall.

The herbicide 2,4-D, which was applied only over the submergent zone, eliminated virtually all of the water milfoil in 1981 but had little effect on coontail. In June 1981, dense patches of coontail were noted in the same locations where it grew in 1980, including areas previously surrounded by water milfoil. During the summer of 1981, the zone which was occupied by water milfoil in 1980 was gradually colonized by muskgrass in the shallower areas and by coontail in deeper areas until nearly all of the suitable habitat (fine substrate) was occupied. In addition to categorizing each zone by the dominant species of macrophyte, zones of coontail were separated into dense (>8 kg/m^2; wet weight) and sparse stands (<3 kg/m^2).

Lake Rush contained a diverse fish assemblage of 17 species dominated by centrarchids (Layzer 1982). Largemouth bass (*Micropterus salmoides*) was the primary piscivorous fish and made up 5 to 23% of all fish collected by electrofishing from 1979 to 1981 (Layzer and Clady 1981). The majority of largemouth bass were 175 to 275 mm (total length) and dietary analysis (n = 114) revealed that sunfishes made up 91% of the total fishes consumed (Layzer et al. 1983).

Materials and Methods

Fish Collections

Sunfishes were collected during eight periods from June to October, 1980, and during seven periods from June to September, 1981. Each sampling period lasted from 2 to 5 days and periods were separated by 7 to 18 days. Fish were caught in unbaited cylindrical minnow traps (6.4-mm wire mesh) which had a funnel opening (2.5 cm) at both ends. Initially, traps were set on the bottom for approximately 24 hours; but beginning in mid-August 1980, and continuing for the remainder of the study, traps were set for an average of 1.62 hours (S.D. ± 0.53).

When each trap was set, water depth was measured to the nearest 10 cm with a metal measuring rod. In shallow areas, substrates were classified visually as fine (principally organic) or coarse (mixture of particle sizes ranging from sand to boulder), and vegetation was pulled up by hand and identified to genus using keys of Fassett (1969) and Muenscher (1967). In deeper areas, substrate was determined by sounds transmitted by the metal measuring rod. Typically, substantial amounts of water milfoil or coontail (the only plants occurring in deeper water) were retrieved with the traps. In 1981 quantitative plant samples (0.2 m^2) were collected at all depths (Layzer 1982). These vegetation samples were dominated by a single species; in fact, 92% of the samples contained only one species. Samples taken in areas classified as having no vegetation did not contain any macrophytes. Distances between adjacent traps varied considerably but were at least 15 m. Traps were set only in habitats that appeared to be homogeneous over an area 10 m^2.

Fish collected from each trap were preserved separately in 10% formalin; later they were measured to the nearest

Table 1

Mean number (± 1 S.E.) of young-of-year sunfishes collected per trap for each sampling period in 1980 (sampling period: E = early; M = middle; L = late).

Sampling period	Number of traps	Mean catch per trap				
		Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
June (M)	52					
July (L)	143	0.04 ± 0.02	1.89 ± 0.33	0.06 ± 0.02	0.08 ± 0.02	0.03 ± 0.01
August (E)	38	0.29 ± 0.17	2.16 ± 0.55	0.37 ± 0.13	0.71 ± 0.22	
August (M)	94	1.13 ± 0.23	1.22 ± 0.30	0.09 ± 0.05	0.20 ± 0.06	0.01 ± 0.01
August (L)	55	1.15 ± 0.23	1.07 ± 0.48	0.20 ± 0.09	0.02 ± 0.02	
September (M)	81	3.30 ± 0.59	3.06 ± 0.67	0.30 ± 0.11	0.17 ± 0.13	0.04 ± 0.03
October (E)	64	3.77 ± 0.78	0.66 ± 0.20	0.06 ± 0.03	0.09 ± 0.05	
October (L)	70	2.27 ± 0.40	0.33 ± 0.10	0.07 ± 0.04	0.06 ± 0.03	
Total fish collected		853	839	75	82	8

millimeter (total length), and identified using descriptions and keys in Cross (1967); Miller and Robison (1973); Pflieger (1975); as well as species-specific characteristics described in Layzer (1982).

Resource Use

Except for six yoy green sunfish captured by electrofishing, all sunfishes used to analyze diets were captured in minnow traps set for 2.2 hours or less. Stomach contents were examined under a dissecting microscope and identified to the lowest possible taxon. Widths of all prey items in a stomach (up to a maximum of 20 of one type) were measured with an ocular micrometer to the nearest 0.1 mm.

For analysis of depth utilization, all data for each year were combined into five depth categories (cm): ≤50, 51–100, 101–150, 151–200, and >200. To compensate for unequal sampling effort, data were standardized by calculating a catch per unit effort (CPUE) for each of the depth categories for each species as follows: CPUE_{ik} = number of species k collected in the ith resource state/number of traps set in the ith resource state. Chi-square tests for differences in probability distributions (Conover 1971) were used to test for differences in the depth and vegetational distributions among species. When more than 20% of the expected values in a contingency table were <5, adjacent categories were combined. For each species, chi-square goodness of fit tests (Conover 1971) were used to test the null hypothesis that the observed catch distributions were the same as the distributions of trapping effort among resource states. The proportion of use (p_{ik}) of a given resource state was found by

$$p_{ik} = \text{CPUE}_{ik} / \sum_{i}^{n} \text{CPUE}_{ik},$$

where n is the number of states in a resource set. The same procedure was used for determining the proportional use of the substrate and vegetation dimensions. The p_{ik}'s obtained in this manner were then used to calculate niche breadth and overlap for each of the habitat dimensions. Niche breadth (B) was calculated by the formula of Levins (1968) as modified by Pianka (1973):

$$B = (1/\sum_{i}^{n} pik^2)/n.$$

A proportional overlap value (O) was calculated following Schoener (1968) to determine the similarity in resource usage between pairs of species:

$$O = 1 - 0.5 \sum_{i}^{n} | p_{ij} - p_{ik} |$$

Results

Relative Abundance

In 1980, 1857 yoy sunfishes were caught in minnow traps (Table 1). Bluegills and redear sunfish were codominant, together making up 91% of the catch. These species also dominated seine collections in 1979 and 1980, but bluegills were 30 to 50% more abundant than redear sunfish (Layzer and Clady 1981). Differences in relative abundance between gears apparently were due to size selectivity. Seines captured more yoy bluegills <30 mm TL, while larger yoy bluegills were more abundant in traps (Layzer 1982). Minnow traps also selected for slightly larger redear sunfish; however, by late August 1980, only 24% of the

Table 2

Mean number (± 1 S.E.) of young-of-year sunfishes collected per trap for each sampling period in 1981 (sampling period: E = early; M = middle; L = late).

Sampling period	Number of traps	Mean catch per trap				
		Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
June (M)	123	0.04 ± 0.03				
July (E)	96	0.10 ± 0.04				
July (M)	142	0.43 ± 0.07	0.09 ± 0.03	0.02 ± 0.01	0.06 ± 0.02	
August (E)	142	1.54 ± 0.17	0.44 ± 0.09	0.15 ± 0.04	0.15 ± 0.04	0.02 ± 0.01
August (M)	96	1.97 ± 0.29	0.86 ± 0.18	0.22 ± 0.08	0.21 ± 0.05	
September (E)	94	2.81 ± 0.35	1.28 ± 0.22	0.10 ± 0.05	0.15 ± 0.05	0.02 ± 0.02
September (L)	96	3.41 ± 0.45	1.07 ± 0.23	0.08 ± 0.04	0.36 ± 0.11	
Total fish collected		1074	381	62	100	5

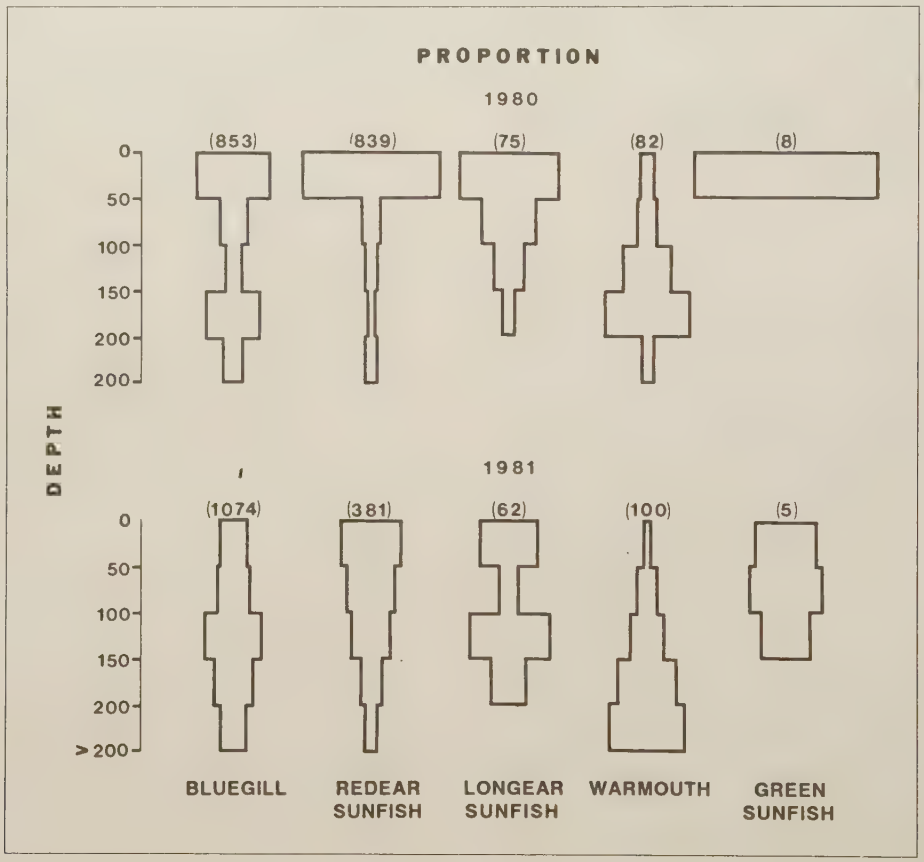

Figure 1

Depth distributions (adjusted for trapping effort) of five species of sunfish collected in minnow traps. Sample sizes are in parentheses.

redear sunfish collected by seining were <30 mm, while 74% of the bluegills in seine hauls were <30 mm. No evidence of selection against the largest yoy sunfishes was observed. In fact, minnow traps captured yearling sunfish of all species up to about 80 mm TL. If size were the only component of gear selectivity, then CPUE of minnow traps probably was an underestimation of the relative abundance of bluegills <30 mm.

In 1981, 1622 yoy sunfishes were captured in minnow traps. Bluegills and redear sunfish again dominated, but

bluegills were nearly three times as abundant as redear sunfish (Table 2). Differences in relative abundance of species between years were primarily due to the significant decrease ($P<0.001$) in numbers of redear sunfish in 1981. Abundance of longear sunfish also declined in 1981 ($P<0.01$), but the CPUE of bluegills and warmouths did not change ($P>0.10$).

Young-of-year sunfishes were first captured in minnow traps in late July 1980 (Table 1). Except for what may have been a sampling artifact in September, CPUE of redear sunfish reached a peak in early August and declined steadily thereafter. In contrast to the trend for redear sunfish, abundance of bluegills steadily increased from early in the season until early October.

Bluegills were captured earlier in 1981 than in 1980, but otherwise their numbers increased as in 1980 (Table 2). In 1981 redear sunfish first appeared in trap catches in mid-July; numbers then increased progressively, peaking in early September. The differences between years suggest that redear sunfish fry hatched later in 1981 than in 1980. Although adult redear sunfish were observed on nests in early April of both years, nests were deserted for an unknown period of time in 1981 when water temperatures dropped from 21°C to 18°C between 9 and 10 April. During this same time, refuge personnel applied the herbicide 2,4-D to Lake Rush. Although male bluegills also deserted nests when the temperature dropped, bluegills reproduced normally during this same period (Layzer 1982). No discernible pattern of abundance was apparent for longear sunfish, warmouth, and green sunfish during either year. Fluctuations in CPUE for these species were relatively small and may have resulted from the combined effects of recruitment, mortality, and sampling error.

Habitat Utilization

The depth distributions of yoy sunfishes differed among species and between years (Fig. 1). In 1980, all species except warmouth were caught proportionately more often in traps set at depths of 50 cm or less. Distribution of bluegills was bimodal with high abundances in the shallowest habitats and at depths between 151 and 200 cm. The concentration of warmouths in deep water generally complemented the distributions of other species. In 1981, all species made greater use of deeper habitats. Although the distribution of redear sunfish was inversely related to depth each year, the proportion collected at depths of 50 cm or less was only 0.32 in 1981 compared to 0.75 in 1980. Longear sunfish used decidedly different depths each year; in 1980 their distribution was unimodal and inversely related to depth, whereas in 1981 their distribution was bimodal and fish were most abundant at depths of 50 cm or less and between 101 and 150 cm. Although few green sunfish were collected each year, they apparently did not use depths greater than 150 cm in 1981. In 1980 green sunfish were collected only from the shallowest habitats.

Table 3

Proportional use (adjusted for trapping effort) of substrate types by young-of-year sunfishes in Lake Rush in 1980 and 1981.

		Substrate	
Species	Year	Fine	Coarse
Bluegill	1980	0.72	0.28
	1981	0.76	0.24
Redear sunfish	1980	0.75	0.25
	1981	0.71	0.29
Longear sunfish	1980	0.03	0.97
	1981	0.17	0.83
Warmouth	1980	0.79	0.21
	1981	0.83	0.17
Green sunfish	1980	1.00	0.00
	1981	0.83	0.17

Longear sunfish were clearly segregated from other species on the basis of substrate (Table 3). Each year longear sunfish used primarily habitats with a coarse substrate; other species were most abundant in areas having a fine organic substrate.

Vegetation was also important in the habitat segregation of yoy sunfishes in Lake Rush. In 1980 most bluegills were collected in habitats containing coontail and water milfoil, but many bluegills were also collected from areas where muskgrass and quillwort (*Isoetes* sp.) grew (Table 4). With the disappearance of water milfoil in 1981, bluegills greatly increased their use of coontail stands. Each year the greatest densities of redear sunfish occurred in habitats where spike rush and muskgrass grew. Microhabitats lacking vegetation were used extensively by longear sunfish each year; in 1981, however, proportionately more longear sunfish were collected by traps set in coontail stands. Although longear sunfish used sparse stands of coontail twice as much as dense stands, the difference was not significant ($\chi^2 = 2.25$, 1 df, $P>0.10$).

In 1980 proportionately more warmouths were collected from habitats containing coontail and American lotus. In 1981 significantly more warmouths were collected from dense stands (wet biomass >8 kg/m^2) of coontail compared to sparse stands (wet biomass <3 kg/m^2) ($\chi^2 = 13.10$, 1 df, $P<0.001$). Nearly all green sunfish were collected from habitats containing muskgrass or spikerush.

Feeding Periodicities

All fishes used in dietary analyses were collected between 0600 and 2100 hours. The mean number of prey per

Table 4

Proportional use (adjusted for trapping effort) of vegetation types by young-of-year sunfishes in Lake Rush in 1980 and 1981.

Plant genera	Year	Species				
		Bluegill	Redear sunfish	Longear sunfish	Warmouth	Green sunfish
Ceratophyllum (dense)	1980	0.28	0.03	0.00	0.22	0.00
	1981	0.31	0.19	0.15	0.62	0.00
Ceratophyllum (sparse)	1981	0.32	0.14	0.33	0.21	0.00
Chara and *Najas*	1980	0.14	0.49	0.00	0.08	0.28
	1981	0.20	0.52	0.13	0.13	0.42
Eleocharis	1980	0.05	0.26	0.07	0.06	0.64
	1981	0.12	0.09	0.08	0.01	0.48
Isoetes	1980	0.14	0.00	0.00	0.00	0.00
	1981	0.00	0.00	0.00	0.00	0.00
Myriophyllum	1980	0.31	0.10	0.04	0.05	0.08
Nelumbo	1980	0.00	0.10	0.00	0.58	0.00
	1981	0.00	0.00	0.00	0.00	0.00
None	1980	0.08	0.02	0.89	0.01	0.00
	1981	0.05	0.06	0.31	0.03	0.10

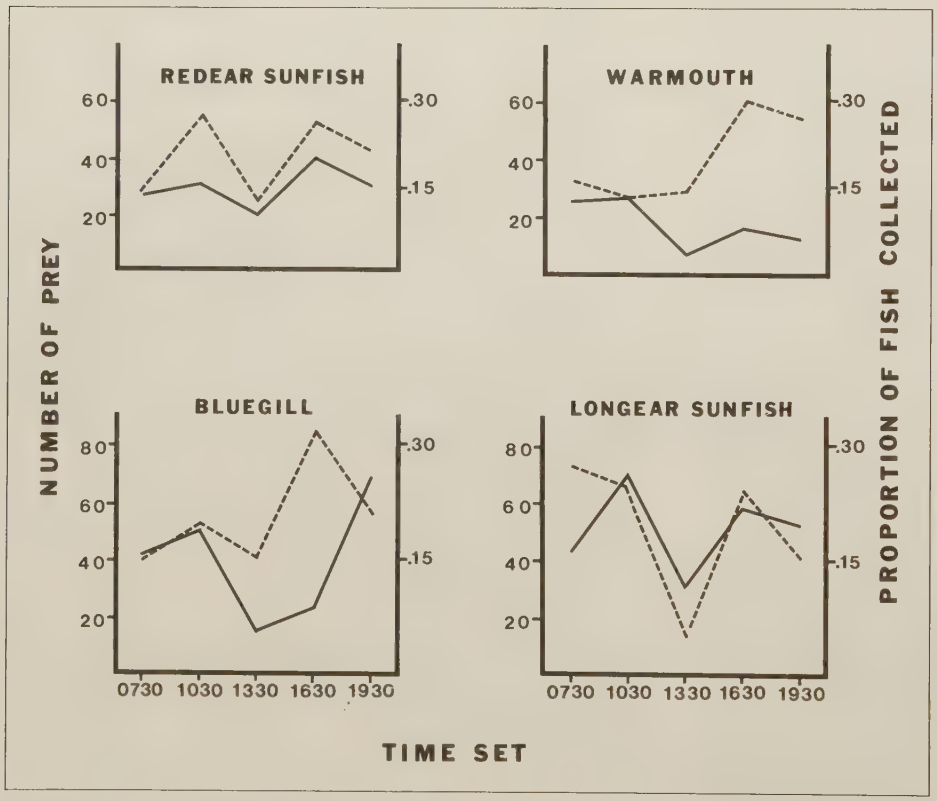

Figure 2

Mean number of prey items in sunfish stomachs (solid lines), and proportion (adjusted for trapping effort) of each species of sunfish collected in minnow traps over time of day (broken line).

stomach was used as a measure of foraging intensity. Data were separated into five 3-h-long periods based on the time of day traps were set. Because few green sunfish were examined and most were captured during the first and last time periods, this species was excluded from this analysis. The remaining species consumed high numbers of prey in mid-morning and late afternoon or evening (Fig. 2). The fewest prey were found in fish of all species caught in the

Table 5

Variation in diets (% numbers) among three individual bluegills and a comparison of diets for 10 individual bluegills collected on the same date and diets of all bluegills collected in 1981. The three individual bluegills were collected by the same minnow trap fished between 1850 and 2005 hours at a depth of 110 cm over a fine substrate in a dense stand of coontail on 1 September 1981.

	Total length (mm)	*N*	Taxa					
			Daphnia sp.	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Individual A	28	1	0.17	0.02	0.47	0.12	0.20	0.02
Individual B	31	1	0.23	0.03	0.12	0.48	0.17	0.01
Individual C	35	1	0.12	0.14	0.38	0.16	0.18	0.01
All bluegills on September 1, 1981		9	0.14	0.08	0.26	0.22	0.26	0.05
All bluegills collected in 1981		62	0.16	0.15	0.23	0.17	0.25	0.04

Table 6

Percentage abundance of each prey item in diets of young-of-year sunfishes in Lake Rush by year.

Species	Year	*N*	Taxa					
			Daphnia sp.	Ostracoda	Chironomidae	Copepoda	Chydoridae	Other
Bluegill	1980	75	14.4	19.2	20.1	6.8	33.5	6.0
	1981	62	16.0	15.2	22.6	16.6	25.5	4.1
Redear sunfish	1980	66	0.7	55.9	12.9	4.6	24.1	1.8
	1981	54	1.1	84.2	7.7	3.2	1.7	2.1
Longear sunfish	1980	43	0.0	62.2	12.4	2.6	22.0	0.8
	1981	43	1.1	55.3	17.4	8.1	15.3	2.8
Warmouth	1980	45	18.9	13.7	58.4	3.2	1.6	4.2
	1981	48	50.1	4.7	11.2	23.6	1.7	8.7
Green sunfish	1980	4	0.0	0.0	40.0	0.0	0.0	60.0
	1981	8	0.0	57.5	5.5	4.8	28.3	3.9

middle of the day. Only bluegills fed mostly near dusk; other species foraged earlier in the evening.

Movement of fishes (as measured by trap catches) generally paralleled trends in feeding intensity, though the greatest catches of bluegills occurred one time period before the peak in stomach contents (Fig. 2). Maximum numbers of prey in warmouth occurred in the morning; in contrast, catches of warmouth in traps were greatest late in the day.

Prey Utilization

A total of 24 types of prey were identified from stomach contents. Most prey items were identified to family (e.g., Chironomidae and Chydoridae) or subclass (e.g., Ostracoda, Copepoda). This absence of taxonomic detail in description of stomach contents yielded conservative estimates of diet separation among sunfishes. Consequently, species with high diet overlap may have greater differences in diets than we estimated and, in like manner, dietary differences may be more pronounced.

No seasonal trends in diets were observed. However, the relative and absolute importance of various prey items did fluctuate over time for a given species and between species for the same sampling period. The variable diets of individual fish collected together (Table 5), suggested that dietary differences between sampling periods could have resulted from chance. Since diets varied among individuals within a sample as much as between samples (Layzer 1982), all food habits data were combined by year. Five prey types generally accounted for over 90% of all food items (Table 6). They were the same prey types that we observed in stomachs of fishes collected by seining but we did not count them. All species of sunfishes ate similar prey, though in different proportions. Ostracods were the most abundant item in the diets of both redear sunfish and longear sunfish. Other sunfishes also ate many ostracods. Diets of warmouths and green sunfish were the most

Table 7
Niche breadth of yoy sunfishes in Lake Rush for various resource dimensions.

Species	Year	Resource dimension			
		Substrate	Vegetation	Depth	Diet
Bluegill	1980	0.83	0.56	0.71	0.76
	1981	0.78	0.49	0.94	0.86
Redear sunfish	1980	0.81	0.38	0.29	0.44
	1981	0.86	0.27	0.80	0.23
Longear sunfish	1980	0.53	0.16	0.41	0.37
	1981	0.71	0.35	0.62	0.49
Warmouth	1980	0.76	0.31	0.60	0.42
	1981	0.71	0.49	0.68	0.51
Green sunfish	1980	0.50	0.26	0.17	0.32
	1981	0.71	0.30	0.59	0.40

variable between years. For instance, daphnids made up only 19% of the diet of warmouths in 1980 but accounted for 50% in 1981. The five major food items were consumed more evenly by bluegills each year; no single item made up more than 34% of their diets.

All species ate prey of similar size, and differences between species in their utilization functions were simply a reflection of the type of prey consumed rather than a result of selecting different sizes of the same prey type. For example, the average width of food items in redear sunfish stomachs was 0.35 mm because ostracods, which made up 56 to 84% of the diet of redear sunfish each year, averaged 0.39 mm in width (Layzer 1982).

Niche Breadth

Bluegills generally showed the broadest resource utilization although niche breadth changed between years (Table 7). Change in depth use was most pronounced for redear sunfish; their niche breadth for depth increased from 0.29 to 0.80. The increase in niche breadth of longear sunfish along the vegetation axis reflected substantially greater use of vegetated habitats in 1981 than in 1980.

The proportional use of the various prey types by redear sunfish changed the most of any species between years, but this change was in contrast to the changes noted in their relative use of habitats. Redear sunfish seemingly foraged over a greater range of habitats in 1981 than in 1980, but became more selective in their feeding.

Niche Overlap

Longear sunfish showed little overlap (all values ≤ 0.31) in 1980, and only slightly higher overlap in 1981 with other species along the substrate axis (Table 8). In contrast, overlap values for use of substrate between all other pairs of species were high (all ≥ 0.72) in both years. Overlap in depth utilization was moderately high (0.55 to 0.75) for six species pairs in 1980 and increased in 1981. There was strong complementarity between the use of vegetation and depth in 1980; five of the ten species pairs overlapped greatly along one habitat axis but little along the other. For example, redear sunfish and longear sunfish used similar depths ($O = 0.74$), but overlapped little ($O = 0.13$) in their use of vegetation. Spatial segregation was less obvious in 1981.

Longear sunfish and redear sunfish had nearly identical diets in 1980; though their diets diverged somewhat in 1981, overlap remained high. Most other species showed changes in diet overlap between years. For example, overlap between redear sunfish and bluegills decreased from 0.63 in 1980, to 0.31 in 1981. Most species appeared to segregate along the vegetation axis in 1980 when nine species pairs had overlaps <0.42. In contrast, only three species pairs had low overlap for use of vegetation in 1981.

Discussion

Partitioning of resources among yoy sunfishes was evident in Lake Rush even though most species were confined to the vegetation. The importance of vegetation type, depth, and diet in segregating species changed between years, indicating a high level of behavioral plasticity for these species. In both years, depth utilization for redears and warmouths yielded essentially mirror images: redear sunfish were most abundant in the shallowest areas, and warmouths were more abundant in the deepest areas. In 1980 overlap between bluegills and redears was moderately high (0.61 and 0.63) for both depth and prey type but low for vegetation type. Moreover, diets of these species varied somewhat at different depths indicating that diets of these

Table 8

Habitat and diet overlaps among young-of-year sunfishes in Lake Rush. (BG = bluegill; RE = redear sunfish; LE = longear sunfish; WM = warmouth; GS = green sunfish).

Species	1980				1981			
	Substrate	Vegetation	Depth	Diet	Substrate	Vegetation	Depth	Diet
BG vs. RE	0.97	0.34	0.61	0.63	0.95	0.67	0.73	0.31
BG vs. LE	0.31	0.18	0.62	0.57	0.41	0.73	0.73	0.60
BG vs. WM	0.93	0.41	0.66	0.57	0.93	0.69	0.64	0.52
BG vs. GS	0.72	0.27	0.36	0.26	0.93	0.37	0.62	0.53
RE vs. LE	0.28	0.13	0.74	0.94	0.46	0.57	0.71	0.71
RE vs. WM	0.96	0.32	0.34	0.34	0.88	0.50	0.46	0.20
RE vs. GS	0.75	0.62	0.75	0.15	0.88	0.56	0.82	0.69
LE vs. WM	0.24	0.10	0.33	0.31	0.34	0.53	0.46	0.28
LE vs. GS	0.03	0.11	0.55	0.13	0.34	0.31	0.66	0.82
WM vs. GS	0.79	0.19	0.09	0.44	1.00	0.17	0.29	0.19

species diverged more when they occurred in the same habitats (Layzer 1982). In 1981 bluegills and redear sunfish were distinctly separated on the basis of diet even though their use of habitat was similar.

High overlap occurred between bluegills and warmouths for both habitat and diet. Perhaps these overlap values approximated the maximum tolerable overlap between these species (Pianka 1972) or these two species may have segregated along an additional dimension or by a finer resolution of diet or microhabitat than recognized. The second alternative is supported by the significantly greater use of dense versus sparse stands of coontail by warmouth while bluegills showed no such difference in use. Moreover, because our estimates of diet segregation are conservative, diets may have been more divergent than we recognized.

In both years, extensive use by longear sunfish of nonvegetated habitats with coarse substrate clearly separated them from other congeners. Together these two habitat dimensions effectively separated longear sunfish from the other four species of sunfishes, which lived primarily in vegetated areas with fine substrates. Use of exposed habitats in Lake Rush by yoy longear sunfish differs from their restriction to shallow vegetated areas in Michigan lakes (Laughlin and Werner 1980). Differences in the distribution of longear sunfish may reflect differences in community composition, specifically within the genus *Lepomis*. The changes in depth distribution of longear sunfish in 1981 indicated that the explanation for their distribution in vegetated and nonvegetated habitats is complex. Increased use of vegetated habitats by longear sunfish in 1981 was probably related both to the decrease in relative abundance of redear sunfish and to changes in the macrophyte community. The differences in depth distribution of redear sunfish and longear sunfish in 1981, and, more importantly, the greater shift towards deeper water by longear sunfish suggest they may have been avoiding areas of high redear abundance. Furthermore, longear sunfish also increased the breadth of their diet in 1981, whereas redear sunfish restricted their diet, thus somewhat reducing niche overlap.

Young-of-year sunfish species, other than longear sunfish, in 1980 remained primarily in vegetation, presumably limiting their risk of predation by largemouth bass. Mittelbach (1988) demonstrated that confinement to the vegetation can result in exploitative competition among juvenile sunfishes. The low growth rates of sunfishes reported in Lake Rush by Layzer et al. (1983) suggest that intra- or inter-specific competition may have been occurring despite the observed partitioning of resources. Sunfish diets may be reflective of exploitative competition. The abundance of ostracods in sunfish stomachs was surprising because Vinyard (1979) found that only 30% of the ostracods ingested by bluegills were digested. Because of their apparent resistance to digestion, it is unlikely that ostracods were a preferred food item even though they were a major item in sunfish diets. Although differential digestion rates of prey may bias food-habits analysis (Gannon 1976), we do not believe that the observed high occurrence of ostracods in sunfish stomachs was due to their resistance to digestion. Head capsules of chironomids are also resistant to digestion; yet, they were uncommon in stomachs of most fishes. Further, ostracods also were abundant in the stomachs of seine caught fishes. We suggest that if yoy sunfishes were competing for food, it was on the basis of quality, and not necessarily quantity, of food items. Perhaps sunfishes are severely limited by food in Lake Rush but receive sufficient nutritional value from ostracods and other prey to meet their basic metabolic demands. Foraging on nutritionally poor prey may be a seasonal survival strategy.

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Comparative Scanning Electron Microscopy Studies of the Egg Envelopes of Six African *Barbus* and Three *Pseudobarbus* Species (Cyprinidae)*

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ABSTRACT

The external morphology of the egg envelopes of six *Barbus* (*B. aeneus*, *B. andrewi*, *B. anoplus*, *B. capensis*, *B. kimberleyensis*, and *B. viviparus*) and three *Pseudobarbus* (*P. afer*, *P. asper*, and *P. quathlambae*) species (Cyprinidae) were studied using scanning electron microscopy. Conventional specimen preparation was used as well as the Cryo technique. Electron photomicrographs and a comparative description of the egg surface sculpturing of these nine species is given. The egg surface ultrastructure of all species is distinct. The honeycomb lattice surface structure of the whitefish (*B. andrewi*), is more similar to that of *P. afer* and *P. asper* than to those of the three yellowfish species studied (*B. aeneus*, *B. kimberleyensis*, and *B. capensis*). The relict redfin minnow, *P. quathlambae*, which only occurs in the upper catchment of the Orange River in Lesotho, does not have a distinct honeycomb lattice. The results indicate that a knowledge of the ultrastructure of the egg envelopes of African cyprinids could be useful for identification of eggs collected from the wild.

Introduction

Cambray and Teugels (1988) have noted that the early life history of the some 2000 African freshwater fishes has received very little attention. The reproductive behaviour of some of the species has been recorded (Lévêque and Daget 1984), however little is known of the ultrastructure of the egg envelopes of the majority of the 2000 species. Even in the North American Great Lakes only 34% of the fish species have had their eggs described (Werner 1976; Johnson and Werner 1986). Studies on the ultrastructure of the envelopes of eggs spawned in freshwater have been somewhat limited (Johnson and Werner 1986) compared to studies on marine fishes.

The egg envelopes of different species have been shown to be ornamented with filaments, spines, patterns of ridges, loops, blebs and pustules (Ahlstrom and Moser 1980; Laale 1980; Boehlert 1984; Matarese and Sandknop 1984). Possibly the morphogenetic activity of individual follicle cells generates these elaborate structures (Wourms 1976). It has been shown for some taxa that these ornamentations and the ultrastructure of the egg envelopes are species specific (Lönning 1972; Ivankov and Kurdyayeva 1973). Therefore the surface structure of the egg envelope in some species can be a useful character for the identification of eggs of different species (Mikodina 1987). However, for many fish species the most difficult ontogenetic stage to identify is the egg and Markle and Frost (1985) argued that few can be identified to the species level. If eggs are found to be distinctive then they can be identified. Researchers will then be able to establish where spawning sites are for specific species, data which will be of value in ecological impact work. Characters associated with the egg envelope have been shown to be highly adapted to the environmental conditions in which the embryo develops (Ivankov and Kurdyayeva 1973; Laale 1980). Matarese and Sandknop (1984) have noted that the main goal of taxonomy with respect to fish eggs is identification and not speculation on the systematic significance of any characters present.

Since there is very little known about the early life history of African freshwater fishes the identification of the egg envelopes of some of the species may provide an important aid in the study of their life histories. In this paper one of the main goals has been to add another set of characters, that is the egg surface ultrastructure, to the present knowledge of African cyprinids. This paper

* The title of NOAA Technical Report NMFS 95 unfortunately does not reflect this single contribution from South Africa. To have included the words "South Africa" in the title of the proceedings might have misled readers into assuming multiple contributions from this country. Managing Editor.

describes and compares the surface structure of the egg envelope of four large and two small *Barbus* species as well as three *Pseudobarbus* species. Scanning Electron Microscopy (SEM) was used as the analytical tool in this investigation as it provides the depth of field necessary to permit visualization of surface structures which are difficult to see using light microscopy.

Methods

Laale (1980), Robertson (1981), Balon (1985), among others have pointed out the confusion and inconsistency in the literature concerning the terminology of fish egg coats. The chorion is the egg coat which envelopes the egg and, in protecting the developing embryo from the external environment (Johnson and Werner 1986), is the major protective coating of the ovum. In many papers the outermost egg envelope of fish eggs is called the chorion without regard to its origin (Shelton 1978). Balon (1985) cautioned that "If the existence of two coats is known, the inner coat should be called zona radiata (cortical coat) and the second or outer coat, chorion (Ivankov and Kurdyayeva 1973; Avni and Soin 1974). If not known, an indifferent term 'egg shell(s) or membrane(s)' should be used." In this paper, to prevent confusion, the covering of the egg is called the egg envelope or egg coat, as it is not known if there are inner and outer egg coats for the species studied. The term egg membrane is not used here, as a true membrane is a thin trilaminar cytoplasmic structure of lipids, proteins, and some carbohydrates that forms the boundary between a cell and its environment (Allaby 1985), whereas the covering of fish eggs is very thick and extracellular.

Eggs for the present study were taken from the growing special collection of early life-history stages housed at the Albany Museum. The eggs were taken from the following developmental series: smallmouth yellowfish (*B. aeneus* Burchell, 1822) (AMG/P 12248); whitefish (*B. andrewi* Barnard, 1937) (AMG/P 12249); chubbyhead barb (*B. anoplus* Weber, 1897) (AMG/P 12255); Clanwilliam yellowfish (*B. capensis* Smith, 1840) (AMG/P 12250); largemouth yellowfish (*B. kimberleyensis* Gilchrist & Thompson, 1913) (AMG/P 12251); bowstripe barb (*B. viviparus*, Weber, 1897) (AMG/P 12252); Eastern Cape redfin (*P. afer* (Peters, 1864)) (AMG/P 12253); Oreodaimon (*P. quathlambae* (Barnard, 1938)) (AMG/P 11224); and the smallscale redfin (*P. asper* (Boulenger, 1911)) (AMG/P 12254). All these series were from known parentage except Oreodaimon eggs which were collected from the wild. Oreodaimon eggs could not be confused with any other fish eggs in the Upper Orange River system in Lesotho (Cambray and Meyer 1988).

Only mature, fertilized ova were used and they were all obtained by stripping gravid females and fertilizing them with the milt from ripe-running males, except for Oreodaimon where wild-collected eggs were used. In the present study only water-hardened, fertilized eggs were used to reduce variability of the observed structural features caused by these two factors. All eggs were fixed in 5% phosphate-buffered formalin. It is noted that in many egg envelope ultrastructure studies the eggs are often fixed in a solution of glutaraldehyde and post-fixed in osmium tetroxide. The majority of the eggs collected during ecological studies by either fisheries biologists or researchers collecting invertebrates are put into buffered or unbuffered formalin. It may therefore be more useful to study formalin fixed material, as the objective of the present study was to assess whether ultrastructural differences in the egg envelopes of African fish eggs can be used as an aid in species identification. Other workers have used a similar approach (Markle and Frost 1985; Olivar 1987).

Table 1
Egg envelope 'pore' size and 'pore' density of four *Barbus* species.

	'Pore' size (μm)	'Pore' density (per 5μm²)
Barbus anoplus	0.29 ± 0.05	29.8 ± 2.58
Barbus capensis	0.20 ± 0.02	50.4 ± 3.58
Barbus kimberleyensis	0.18 ± 0.02	9.8 ± 0.45
Barbus viviparus	0.27 ± 0.04	18.2 ± 1.48

The eggs were prepared using conventional techniques, involving a graded series of ethanol, transitional solvents, amyl acetate, and critical point drying (Cross 1987). The specimens were sputter-coated with gold and examined in a JEOL JSM-840 Scanning Electron Microscope operating at 10 KV.

Distortion during dehydration of biological specimens is a major problem when viewing SEM material, therefore a second method was used. The phosphate-buffered formalin-preserved eggs of three species were prepared using the Cryo technique. This technique is usually used to observe small delicate specimens in a frozen hydrated state. This method minimizes distortion. However, distortion can occur with ice crystal formation and the deposition of frost on the specimen surface (Cross 1987). Sub-cooled nitrogen was prepared in a vacuum chamber. Air was admitted to the vacuum chamber and the surface-dried eggs were fixed on stubs, rapidly quench-frozen in the nitrogen, and left to freeze for two minutes. The eggs were then taken to a chamber of the JEOL JSM-840 SEM unit which had been cooled by liquid nitrogen. The specimens were metal coated and viewed (Cross 1987). This method does not remove the mucous from the egg surface and was used as a comparative method to the more conventional method outlined above.

The measurement of the polygons of the honeycomb patterns of the egg envelopes was done from the photomicro-

Table 2
The size of the honeycomb cells (polygon units), pattern units, and cell walls of *B. andrewi*, *P. afer*, and *P. asper*.

	Cell width (μm)			Cell wall width (μm)		
	Mean	SD	Range	Mean	SD	Range
Barbus andrewi (n = 30)	1.53	0.23	1.08–1.94	0.47	0.11	0.29–0.72
Pseudobarbus afer (n = 30)	1.27	0.12	1.08–1.44	0.53	0.12	0.36–0.79
Pseudobarbus asper (n = 30)	1.61	0.15	1.44–2.16	0.50	0.08	0.36–0.74

graphs and taken along the greatest axis, using a calibrated eyepiece micrometer in a binocular microscope. The thickness of the cell walls and the diameters of the pores were measured with the eyepiece micrometer. The number of pores per square unit were counted using a five μm square grid randomly put on the photomicrograph (6000 ×) for five independent counts of all the pores within the grid.

Results

Ultrastructure of the Egg Envelope

Whitefish (*B. andrewi*)—Water-hardened eggs of whitefish are spherical and 2.09 ± SD 0.07 mm in diameter. The surface of the egg envelope is characterized by a honeycomb lattice pattern (Fig. 1a). The individual pattern units are usually five-sided although there are cells with three to six sides and there are also several round and oblong cells. The actual cell walls are better outlined than those of the two *Pseudobarbus* species. There is also a greater cell depth than that of the *Pseudobarbus* species.

Chubbyhead barb (*B. anoplus*)—Cambray (1983) gave the size of water-hardened chubbyhead barb eggs as 1.1 mm in diameter. The egg envelopes of *B. anoplus* are highly adhesive (Cambray 1983). The surface of the egg envelope is covered with roundish 'pores' or pits. Since cross sections of these eggs have not been done it is not possible to distinguish between pores and pits, therefore in this paper the descriptive term 'pore' is used. Manner et al. (1977) used electron microscopy to determine that the pores did not penetrate the egg envelope of *Pimephales promelas*. The 'pores' are 0.29 ± SD 0.05 μm in diameter and are sunken on the surface of the egg envelope (Fig. 1b). The 'pores' are fairly evenly distributed and there are approximately 29.8 ± SD 2.58 per 5 μm^2 (Table 1).

Eastern Cape redfin (*P. afer*)—Water-hardened eggs of the Eastern Cape redfin are 1.56 ± 0.08 mm in diameter with a small perivitelline space. The surface of the egg envelope is covered with a relatively shallow honeycomb network (Fig. 1c) compared with whitefish (Fig. 1a). The dimensions of the cells and cell walls are given in Table 2. The individual pattern units are fairly uniformly 'round' surrounded by five to six other cells.

Smallscale redfin (*P. asper*)—Water-hardened eggs of the smallscale redfin are 1.12 ± 0.05 mm in diameter with a small perivitelline space. The surface of the egg envelope is covered with a honeycomb network of cells similar to the Eastern Cape redfin. The dimensions of the cells and cell walls are given in Table 2. Each cell has either five or six sides (Fig. 1d).

Oreodaimon (*P. quathlambae*)—Water-hardened eggs of Oreodaimon are 1.8 ± SD 0.09 mm in diameter with a small perivitelline space (Cambray and Meyer 1988). Unlike the Eastern Cape redfin and the smallscale redfin, the surface of the egg envelope of Oreodaimon is not covered by a honeycomb structure. There are faint round markings on the surface of the egg envelope (Fig. 1e), which are 0.75 ± SD 0.10 μm in diameter.

Clanwilliam yellowfish (*B. capensis*)—Water-hardened eggs of the Clanwilliam yellowfish are 2.76 ± SD 0.13 mm in diameter. The egg has no surface ornamentation except for 'pores' which are 0.20 ± SD 0.02 μm in diameter and fairly evenly spaced with 50.4 (46–55) 'pores' per square unit (Table 1; Fig. 1f).

Largemouth yellowfish (*B. kimberleyensis*)—Water-hardened eggs of the largemouth yellowfish are 3.31 ± SD 0.26 in diameter. The surface of the egg envelope is relatively smooth and there are comparatively few 'pores' on the egg envelope (Fig. 1g). The 'pores' have a diameter of 0.18 ± SD 0.02 μm and are quite evenly distributed with 9.8 (9–10) 'pores' per square unit (Table 1).

Bowstripe barb (*B. viviparus*)—Water-hardened eggs of the bowstripe barb are 1.0 mm in diameter with a 0.2 mm

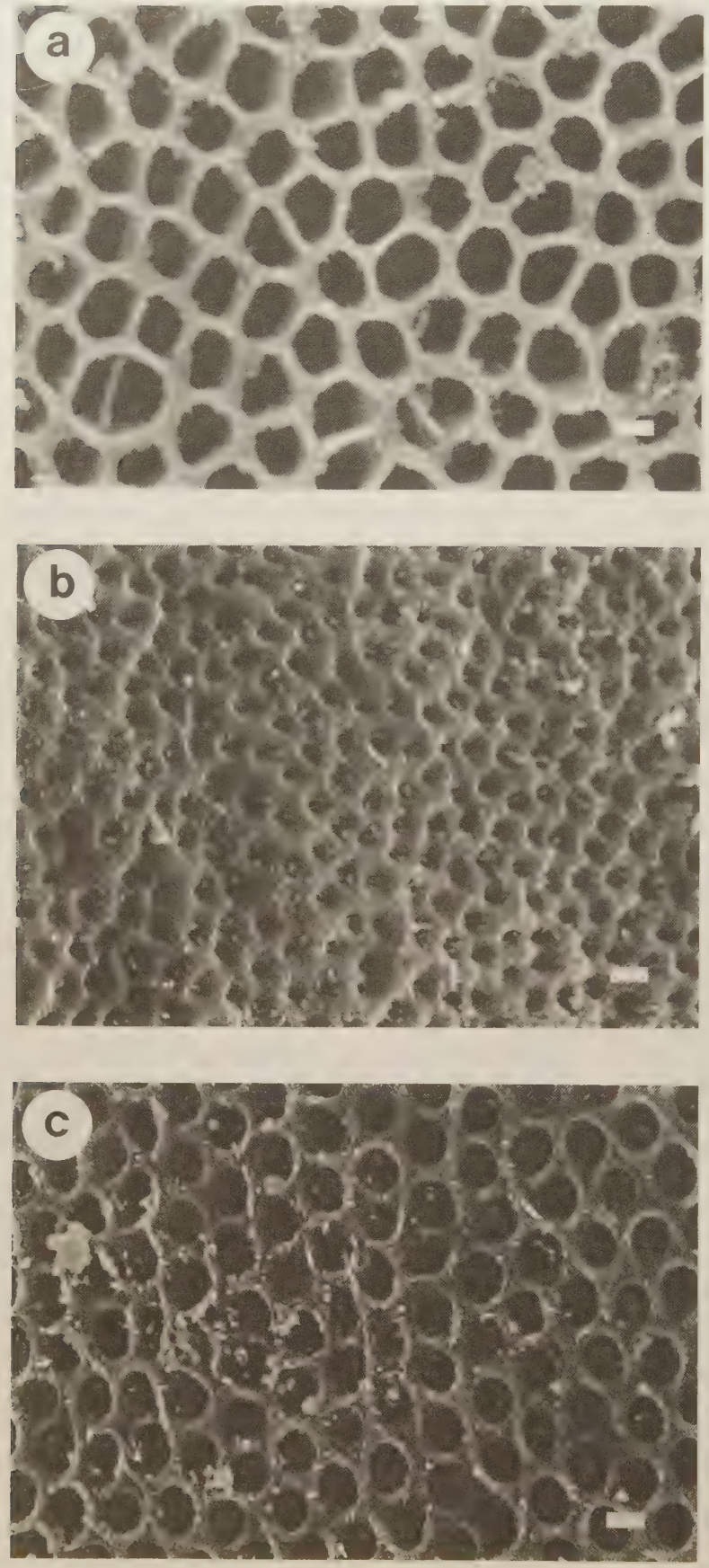
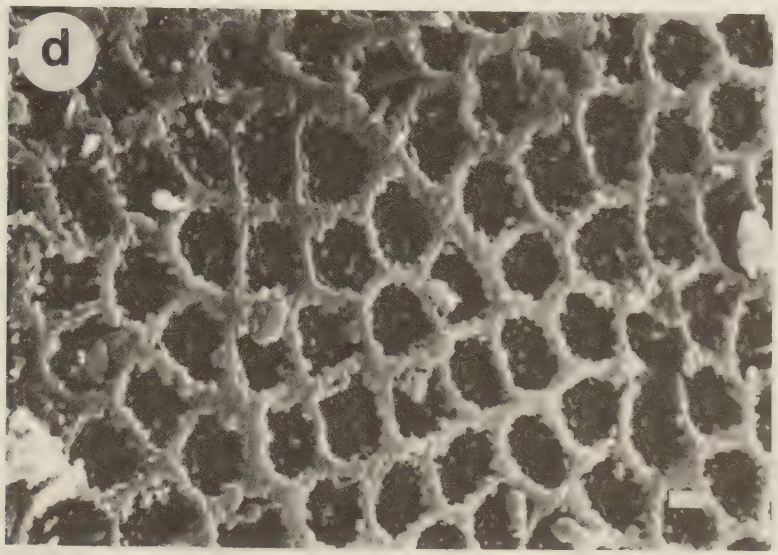
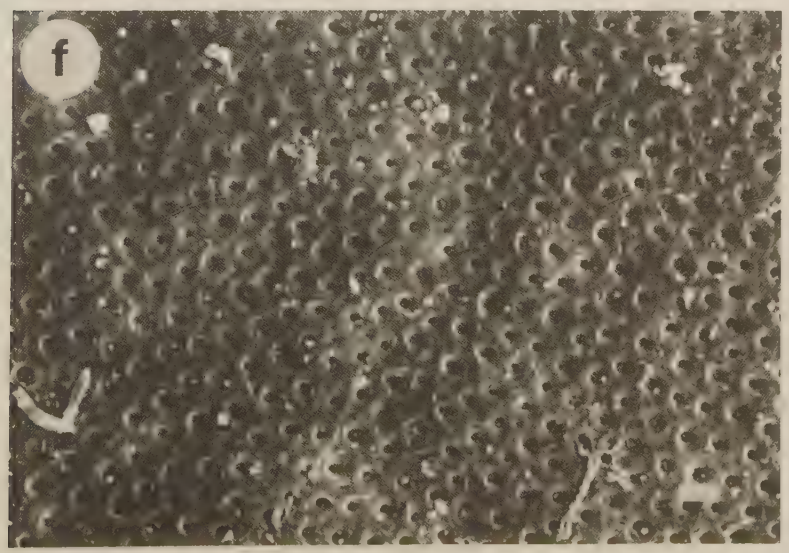


Figure 1

SEM photomicrographs of the ultrastructure of the egg envelope of the following species, eggs (**a–h**) prepared by conventional means, (**i**) prepared by Cryo technique: (a) Whitefish (*B. andrewi*); (b) Chubbyhead barb (*B. anoplus*); (c) Eastern Cape redfin (*P. afer*); (d) Smallscale redfin (*P. asper*); (e) Oreodaimon (*P. quathlambae*); (f) Clanwilliam yellowfish (*B. capensis*); (g) Largemouth yellowfish (*B. kimberleyensis*); (h) Bowstripe barb (*B. viviparus*); (i) Smallmouth yellowfish (*B. aeneus*). Scalebar = 1 μm.





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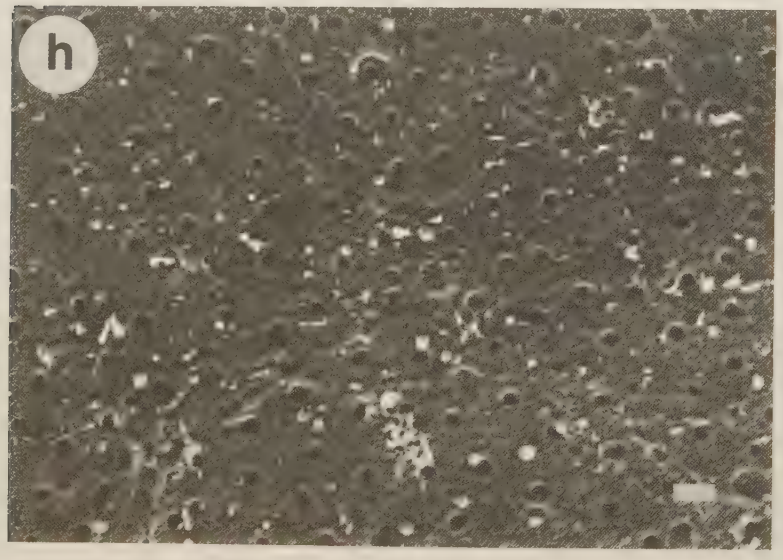

Figure 1—*Continued*

perivitelline space (Ferguson 1987). The scattered 'pores' (Fig. 1h) have a diameter of 0.27 ± SD 0.04 μm with 18.2 (16–19) 'pores' per square unit (Table 1).

Smallmouth yellowfish (*B. aeneus*)—Water-hardened eggs of smallmouth yellowfish are approximately 3.1–3.4 mm in diameter (Groenewald 1961). The conventional preparation technique was not successful and the Cryo technique was useful for this species. The surface of the egg was smooth and had pores or pits (Fig. 1i). The 'pores' on the smallmouth yellowfish were not compared with the size and density of the 'pores' on the eggs of other species because only the Cryo technique was successful for this species.

Comparison of SEM Techniques

The Cryo technique was used on the eggs of a few species to compare with the conventional critical point drying (CPD) method. CPD prepared whitefish eggs show the typical honeycomb pattern (Fig. 1a), while the mucous remains on eggs prepared with the Cryo method (Fig. 2a). The same is seen for the redfin minnows (Figs. 1, c and d; 2, b and c). It has been noted that the fixation methods used in electron microscopy tend to dissolve the mucous coating more or less completely (Lönning and Hagström 1975). The mucous layer on the highly adhesive eggs of *B. anoplus* prepared with CPD is not present (Fig. 1b). In addition the structures are left intact using the Cryo technique and are not as 'eroded' as they were for the conventionally prepared eggs (*compare* Figs. 1d and 2c).

Discussion

Egg Envelope Microstructure

The outer egg envelope microstructure in some species is formed by follicle cells during oogenesis (Sponaugle and Wourms 1979; Stehr 1979; Stehr and Hawkes 1983) giving rise to patterns which may be seen in ovarian eggs. However, the pattern seen on ovarian eggs of certain species can be radically different from those observed on water-hardened, fertilized eggs (Lönning et al. 1984). Morphological changes may occur in the ultrastructure of the egg envelope of certain species during embryogenesis. Manner et al. (1977) found these changes were observed on the outer and inner surfaces as well as in the cross section.

There is great diversity in the structure of the egg envelopes from different species of teleosts in thickness, number of lamella, and surface structure. Most fish eggs have smooth unornamented egg envelopes; however, in some species it can be elaborately ornamented (Ahlstrom and Moser 1980). The most widespread type of egg envelope ornamentation is a honeycomb-like polygonal network found on the outer surface of the egg envelope (Ahlstrom and Moser 1980). The most common network structure is hexagonal but in some species the polygons can have 4, 5, or 7 sides which are intermixed with the more usual 6-sided pattern. In the present study this pattern was observed in whitefish (Fig. 1a), which has deep cell units compared with the shallow honeycomb structure of the redfin minnows examined (Figs. 1, c and d).

Boehlert (1984) suggested that studying the structure of the egg envelope on ovarian eggs could prove useful in the identification of marine plankton samples. Since the egg envelope ultrastructure of most African freshwater fishes is not known, SEM work of developing ovarian eggs may be useful in discerning differences in eggs collected from the wild and may aid in the identification of these samples. But care should be taken in case there are major changes after fertilization and water-hardening.

In a freshwater study, Riehl (1979) prepared identification keys based on the structural peculiarities of the egg envelopes of several freshwater fishes. The egg envelopes of the silver carp (*Hypophthalmichthys molitrix*), bighead (*Aristichthys nobilis*), the grass carp (*Ctenopharyngodon idella*) and the black carp (*Mylopharyngodon piceus*) are distinguished by their species-specific structural features (Mikodina and Makeyeva 1980). In another study on the eggs of freshwater fishes, Keevin et al. (1980) used egg envelope ornamentation to distinguish genera of killifishes. Johnson and Werner's (1986) study on the ultrastructure of the egg envelopes of five freshwater fish species was initiated so that researchers could distinguish between the eggs of key species in order to assess the environmental impact of energy-generating facilities and other perturbations on spawning and nursery grounds. Knowledge of egg envelope ultrastructure in African fishes would also be of value in environmental impact studies.

The envelopes of certain marine teleost eggs have a morphology which is species specific (Lönning and Hagström 1975). Mikodina (1987) found that the structural characteristics of the egg envelope surface can be used as taxonomic traits for the pelagic eggs of several marine fish species. Some authors contend that in many groups of fishes the structure of the egg envelope may be an indication of the systematic status of the species (Rass 1953; Ivankov and Kurdyayeva 1973). In this preliminary paper the egg envelope ultrastructural characters discussed are only considered for egg identification.

'Pore' Size and Density

Olivar (1987) found that in some marine fish eggs, pore size varied little between species, but pore density differed markedly. In the species Lönning (1981) examined, both pore diameter and the number of pores varied. In the present study both 'pore' diameter and density varied between species (Table 1). However, 'pore' density dif-

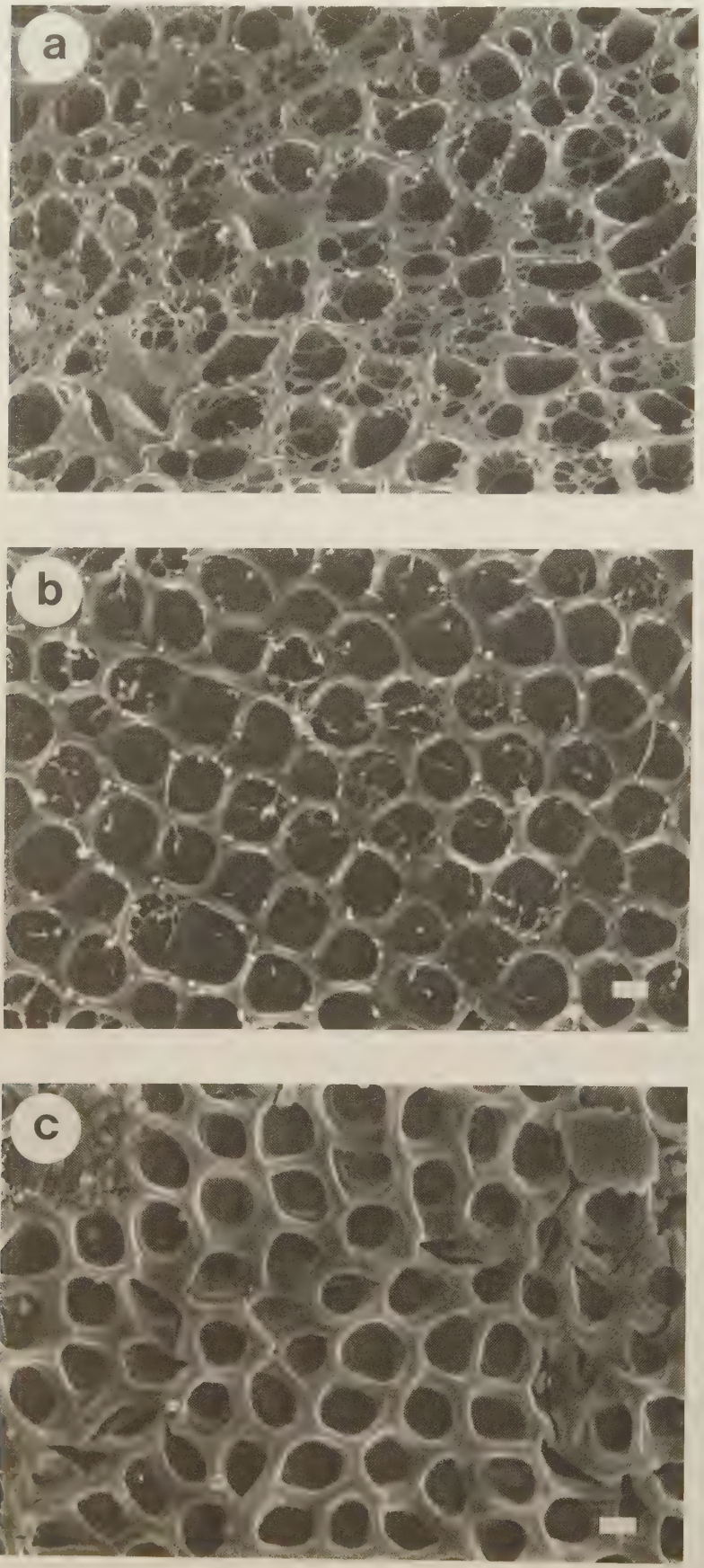

Figure 2
SEM photomicrographs of the ultrastructure of the egg envelope prepared using the Cryo technique for the following species: (**a**) Whitefish (*B. andrewi*); (**b**) Eastern Cape redfin (*P. afer*); (**c**) Smallscale redfin (*P. asper*). Scalebar = 1 μm.

fered more markedly than did 'pore' diameter, a finding which is similar to the findings of Olivar (1987). The appearance of the 'pores' is distinct in the *Barbus* species studied here, varying in size and number per square unit. The 'pore' diameter is smallest in the largemouth yellowfish egg envelopes (0.18 μm) and the largest 'pores' were observed on the egg envelopes of *B. anoplus* eggs (0.29 μm) (Table 1). The greatest number of 'pores' per square unit were found on the whitefish eggs ($50.4/5\mu m^2$) and the least number on the largemouth yellowfish eggs ($9.8/5\mu m^2$) (Table 1).

Care must be taken with the interpretation of pore structure because morphological changes after fertilization can be accompanied by changes in the surface structure of the egg coat (Perry 1984). Different preparation techniques (CPD vs. Cryo) can cause varying distortions. In the present study, smallmouth yellowfish eggs were prepared using only the Cryo technique owing to distortions using the CPD method. Mikodina (1987) cautioned that the structural characteristics of pores on the egg envelope are considered unreliable criteria for the identification of eggs (Mikodina 1987). In a study of the egg envelope structure of *Pseudopleuronectes americanus*, Perry (1984) found that the average distance between the pores and pore diameter decrease after fertilization, possibly because of the final levelling and hardening of the egg envelope after fertilization. Hagström and Lönning (1968) have also demonstrated that there is a change in the pores of certain species after insemination of the egg.

After fertilization and hardening in sea water the surface of the egg envelopes of lumpsucker eggs (*Cyclopterus lumpus*) were no longer smooth and covered with regularly distributed pores but became characterized by ridges and almost completely covered by papillae (Lönning et al. 1984). Obviously one needs to take care in the interpretation of surface structures and indicate whether the eggs have been fertilized and water-hardened.

Pseudobarbus Species

The redfin minnows of southern Africa are distinctive and at a specific level are not obviously similar to other southern African *Barbus* species; therefore the flexible-rayed redfins were removed from the genus *Barbus* and put into the genus *Pseudobarbus* (Skelton 1980, 1988). Oellermann (1988) showed that chromosome counts of the Eastern Cape redfin was 96. He therefore placed the redfin minnows with the group of cyprinids showing tetraploidic origins. The Eastern Cape redfin and the smallscale redfin are closely related (sister species: Skelton 1988) and it has been shown in the present study that their egg envelope ultrastructure is similar and distinctive (Fig. 1, c and d). In contrast the egg envelope structure of the more distantly related redfin minnow, Oreodaimon, does not have a honeycomb pattern of ridges (Fig. 1e). The redfin minnow egg envelope surface patterns are unlike the patterns observed on the two small *Barbus* species examined here. Skelton (1980) suggested that of all the *Barbus* species in southern Africa the chubbyhead barb; Marico barb (*B. motebensis*); and the redtail barb (*B. gurneyi*) are most similar to the flexible-rayed redfins (for example, the Eastern Cape, smallscale, and Oreodaimon redfins). The chubbyhead barb does not have the honeycomb structured egg envelope as do two of the redfins, but a more simple egg surface covered with 'pores.' In addition the chubbyhead barb is clearly diploid compared to the tetraploid redfins (Oellermann 1988).

Ecological Notes

It has been suggested that superficial similarity of egg envelope structure on phylogenetically distant genera supports a functional role (Robertson 1981) and independent derivation (Boehlert 1984). One would expect differences in egg surface ultrastructure because of the range in habitat and breeding habits of teleosts (Kuchnow and Scott 1977). Surprisingly, in their study of the egg envelopes of 40 fish species belonging to 8 orders, Ivankov and Kurdyayeva (1973) demonstrated that it is not correct to put overriding significance on the mode of spawning and the nature of the spawning grounds on the structure of the egg envelope thereby supporting the findings of Rass (1953).

Some authors have suggested that there can be differences in the egg envelope structures in fishes of the same ecological group. For example, a thin gelatinous membrane attaches eggs to submerged vegetation in fishes of the family Cyprinidae whereas villi serve this purpose in the "lake minnow" and a long filament in the "rotan" (Ivankov and Kurdyayeva 1973). Whereas Mikodina (1987) has shown that different fish species developing in similar ecological conditions have similar egg envelope structures.

The conservative structure of the egg envelope has been noted in fishes with different spawning ecology and different types of eggs (pelagic or benthic). Examples given by Ivankov and Kurdyayeva (1973) were several silurids which lay eggs on a different substrate for each species yet in all species the egg envelope was represented by a thick honeycomb pattern. The structure of the egg envelope may be an indication of the systematic status of some species because they found a similarity in the structure of the egg envelope of fishes of the same systematic group although the fish lay their eggs on different substrates (Rass 1953; Ivankov and Kurdyayeva 1973). Ivankov and Kurdyayeva (1973) suggested that the structure of the vitelline 'membrane' was due to its protective function whereas the structure of the outer egg envelope, the chorion, was an indication of the systematic status of the species.

Ivankov and Kurdyayeva (1973) noted that fishes of the family Cyprinidae are mainly phytophilous. The fish species examined in the present study were riverine species and in the family Cyprinidae. All the eggs examined were

demersal (substratum) eggs. The chubbyhead barb (Cambray 1983) and the bowstripe barb (Ferguson 1987) have adhesive egg envelopes. The three redfin minnows have slightly or nonadhesive egg envelopes (Cambray and Meyer 1988; pers. obs.). Species such as the redfin minnows breed in the riffle areas after rains (Cambray and Meyer 1988). The redfin minnows put their nonadhesive eggs under boulders whereas the chubbyhead and bowstripe barbs are more typically phytophilous (Cambray and Bruton 1984; Ferguson 1987).

It has often been said that the primary function of the outer egg envelope is to protect the embryo from the external environment (Manner et al. 1977; Groot and Alderdice 1985). In many species egg envelope thickness can often be related to the environment where the eggs are found, such as the thick envelope of some species of demersal eggs compared with thinner envelopes in certain pelagic eggs (Lönning 1972; Stehr and Hawkes 1983). It is now necessary to examine the depth and number of egg envelopes of African cyprinids.

Conclusion

The main objective of this preliminary paper on the ultrastructure of the egg envelopes of several African *Barbus* and *Pseudobarbus* species was to assess whether or not Scanning Electron Microscopy would prove a useful analytical tool in identifying eggs collected from the wild. The results from this study provide encouragement for further work in that each of the nine species examined showed distinctive egg envelope ultrastructures, most notably the redfin minnows and the whitefish. For example, if egg collections of several minnow species (such as the co-occurring species, small-scale redfin and the chubbyhead barb) were made at the same time in the Groot River, Gamtoos River System of the Cape Province, the eggs could be positively identified by using Scanning Electron Microscopy. The Cryo technique is a useful method to prepare eggs for viewing in the SEM, especially if one wants to observe the mucous covering and its position on the egg coat. The Albany Museum has initiated a collection of SEM photomicrographs of the ultrastructure of the egg envelopes of African freshwater fish species to augment their early life-history collections.

Acknowledgments

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Effects of Fixation and Dehydration on Shrinkage and Morphology in Common Snook Yolk-Sac Larvae

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ABSTRACT

Five fixatives (Bouin's, Davidson's, phosphate buffered glutaraldehyde and paraformaldehyde, and 10% formalin/seawater) were compared to evaluate mean notochord length (MNL) shrinkage of yolk-sac larvae of the common snook (*Centropomus undecimalis*). Measurements were taken at initial fixation, after 90 days' storage in fixative, and after serial dehydration. Larvae fixed in Bouin's solution and Davidson's solution shrank 9.05% and 11.49% in mean notochord length. The MNL of larvae fixed in glutaraldehyde for 90 days was not significantly different from the MNL of live larvae; however, MNL decreased 12.67% following dehydration. Paraformaldehyde-fixed larvae had a maximum shrinkage of 5.06% at 90 days; dehydration resulted in total shrinkage of 16.74%. Larvae fixed in formalin/seawater shrank 5.86% at 90 days; dehydration resulted in total shrinkage of 12.08%. Observations were made of changes in the morphological appearance of larvae preserved in various fixatives.

Introduction

The length of fishes collected in the field is one of the most common parameters used in examining the life history of a species. Length-frequency analyses have been used to determine growth (MacDonald and Pitcher 1979; Schnute and Fournier 1980) as well as ontogenetic shifts in habitat (Gilmore et al. 1983; Brandt 1986); diet (Laroche 1982; Govoni et al. 1983; Peters and McMichael 1987); and feeding chronology (Brandt 1986). Stock-assessment methods and determination of recruitment are often based on length-frequency analyses (Jones 1984; Pauly and Morgan 1987), although it is realized there are serious shortcomings with length-frequency analysis (Basson et al. 1988) because the differential treatment of collections may compromise the accurate assessment of true (live) length.

Most marine fish larvae are fixed and preserved in formalin-based solutions that may be buffered, mixed with acids and/or alcohol, or diluted with seawater. Phosphate-buffered formalin solutions are preferred to solutions buffered with borax or limestone because they minimize shrinkage; dampen pH changes; and prevent pigment loss, decalcification, and demineralization (Farris 1963; Taylor 1977; van der Veer 1982; Lavenberg et al. 1984; Markle 1984; Tucker and Chester 1984). Formalin-mixed solutions such as Bouin's and Davidson's fluids, which contain acid components, also have been recommended because they maintain cellular integrity at the light microscope level and because they ensure minimal shrinkage of fixed tissue (Stickland 1975; Theilacker 1980; Hinton et al. 1984). Formalin solutions in seawater are used extensively because of their convenience in the field. Although distortion of preserved tissue may be minimal initially, shrinkage of tissue in fixative increases over time and increases significantly with subsequent dehydration (Parker 1963; Rosenthal et al. 1978; Schnack and Rosenthal 1978; Hay 1981, 1982; Tucker and Chester 1984).

Few studies have investigated the fixative-induced shrinkage in yolk-sac larvae. Farris (1963) observed the effects of borax-buffered 3% formalin/seawater solution over a 6-week period; Schnack and Rosenthal (1978) and Rosenthal et al. (1978) studied the effects of 2% and 4% formalin/seawater solutions over a 20-day period and for a period of more than 1 year, respectively. Formalin has also been found to have a differential effect on yolk and tissue (Heming and Preston 1981).

In this study we evaluate the shrinking of newly hatched snook larvae (*Centropomus undecimalis*) at initial fixation, after storage in fixative, and after a graded alcohol dehydration. Five fixative solutions commonly used at field stations and laboratories are compared. Larvae used in this study came from a single spawn and had not absorbed their yolk sacs.

This homogeneous group provided a means for gathering shrinkage data from larvae in a primary developmental stage prior to first feeding. In live larvae observed at this stage, tissues are translucent with visible dendritic and condensed chromatophores. Internal organs are easily observed. Two regimes were used to evaluate shrinkage: A) larvae fixed and subsequently dehydrated within 6 days of initial fixation for storage in 70% ethanol and B) larvae retained in fixative for 90 days.

Materials and Methods

Four hundred laboratory-spawned common snook larvae were collected live 18–24 hours after hatching in 2-liter beakers and were individually placed by pipette onto ring slides. Care was taken to minimize damage during handling because such damage could promote shrinkage prior to live measurement and fixation (Theilacker 1980). Anesthesia, which has been shown to contribute to shrinkage in live larvae (Parker 1963; Theilacker 1980), was not used. Measurements were taken to the nearest 0.01 mm of notochord length (NL). Each larva was measured in a small drop of seawater of sufficient size to keep the larva alive; an ocular micrometer was used at 40 × for measurements, and all live and subsequent measurements were made by the same person. Individual larvae were placed live in numbered vials of approximately 1-mL fixative volume.

Fixatives used in the study were as follows:

- Bouin's fluid (Sheehan & Hrapchak 1980)

Saturated picric acid (21 gm to 1 liter) in distilled water	1500 mL
Formalin	500 mL
Glacial acetic acid	100 mL

- Davidson's fluid (Yevich and Barszcz 1977)

Formaldehyde (40% solution)	200 mL
Glycerin	100 mL
Ethanol (95% solution)	300 mL
Glacial acetic acid	100 mL
Water (distilled or seawater)	300 mL

(Davidson's is cloudy when mixed with seawater with high salinity. Distilled water was used in preparation of fixative for this study.)

- 3% glutaraldehyde in 0.1 M phosphate buffer (made with monobasic and dibasic sodium phosphate - pH 7.4)
- 10% paraformaldehyde in 0.1 M phosphate buffer (made with monobasic and dibasic sodium phosphate - pH 7.4)
- 10% formalin in seawater (seawater salinity - 29.5 ‰, collected from larval incubation cone).

Fixatives were prepared within 24 hours of use, and pH was determined initially and after 90 days. The total sample was divided into two groups of 200 each (Groups A and B). Each group was composed of 5 subgroups of 40 individuals; each subgroup represented one of the five fixatives being studied. The vials were stored at room temperature for subsequent measurements.

Group A

After 3 days in fixative, larvae were remeasured. Fixative solution was removed by pipette, and serial dehydration was begun in 30% ethanol, which was changed to 50% and then 70% ethanol, and 24 hours allowed between changes. Each larva was measured at the time of alcohol change and after the larva had been in 70% ethanol for 24 hours. Group A samples were then stored at room temperature.

Group B

Group B samples were remeasured 30, 60, and 90 days after fixation. No solutions were changed.

Statistical Testing

Initial shrinkage was tested for treatment effect using a Model I one-way analysis of variance (ANOVA; Sokal and Rohlf 1969). Because subsequent measurements were made on the same individuals, we could not assume independence of the error term. Overall treatment effect was, therefore, tested using a repeated measures model (Winer 1971). Data analyses were completed using SAS utility programs on Florida Department of Natural Resources' IBM 4341 Group II System computer. All tests for significance were performed at the 95% level ($P<0.05$).

Results

Bouin's and Davidson's Fluids

Effect of Fixation and Subsequent Dehydration—Fixation in Bouin's resulted in significant larval shrinkage (10.04%; Table 1); there was, however, little change in mean notochord length (MNL) following serial dehydration (Fig. 1). Larvae fixed in Davidson's and serially dehydrated to 70% alcohol shrank 13.48% (Table 1; Fig. 1). Larvae shrank approximately one percent following each treatment.

Effect over Time—Larvae fixed in Bouin's and Davidson's fluids shrank 9.05% and 10.21% (Table 1) by 30 days after fixation, but little change in MNL was recorded in subsequent measurements for either fixative (Fig. 2). Initial shrinkage was significant. A maximum shrinkage

Table 1

Shrinkage due to fixation and ethanol dehydration (Group A) and over time without fixative change (Group B). Mean notochord length in millimeters (percent shrinkage).

	Group A					Group B			
	Live	3 days	30% Etoh	50% Etoh	70% Etoh	Live	30 days	60 days	90 days
Bouin's	2.39	2.15 (10.04)	2.14 (10.46)	2.13 (10.88)	2.13 (10.88)	2.32	2.11 (9.05)	2.10 (9.48)	2.11 (9.05)
Davidson's	2.30	2.10 (8.70)	2.05 (10.87)	2.02 (12.17)	1.99 (13.48)	2.35	2.11 (10.21)	2.09 (11.06)	2.08 (11.49)
Phosphate Buffered Glutaraldehyde	2.37	2.32 (2.11)	2.33 (1.69)	2.20 (7.17)	2.07 (12.67)	2.35	2.35 (0.00)	2.35 (0.00)	2.35 (0.00)
Phosphate Buffered Paraformaldehyde	2.39	2.30 (3.77)	2.30 (3.77)	2.16 (9.62)	1.99 (16.74)	2.37	2.27 (4.22)	2.26 (4.64)	2.25 (5.06)
10% Formalin/ Seawater	2.40	2.32 (3.33)	2.28 (5.00)	2.18 (9.17)	2.11 (12.08)	2.39	2.29 (4.18)	2.29 (4.18)	2.25 (5.86)

of 9.05% in Bouin's and 11.49% in Davidson's was recorded at 90 days. The initial pH of Bouin's fluid was 1.9 and had changed to 2.3 after 90 days. The initial pH of Davidson's fluid was 2.7; it had fallen to 2.5 after 90 days.

Morphological Changes—After fixation in Bouin's, formerly translucent larvae turned golden yellow and pigment markings disappeared. Viscera visible in live animals were no longer distinguishable. After these larvae were dehydrated to 70% ethanol, the yellow color lightened somewhat and internal morphology was more discernible. Tissue color of larvae fixed in Davidson's changed to light brown and pigment markings disappeared, but external morphology and viscera were more visible than in Bouin's.

3% Glutaraldehyde in 0.1 M Phosphate Buffer (pH 7.4)

Effect of Fixation and Subsequent Dehydration—No significant difference in MNL was found between live larvae and the same animals measured 3 days after fixation (Fig. 1). Mean notochord length, however, decreased by 7.17% in 50% ethanol and by 12.67% in 70% ethanol (Table 1).

Effect over Time—Mean notocord length decreases were not observed (Fig. 2; Table 1). Measurements made at 90 days may have been compromised because the posterior end of the notochord was not clearly distinguishable because of tissue opacity. The initial fixative pH was 7.6; it had changed to 7.1 after 90 days.

Morphological Changes—A heavy precipitate formed during fixation, adhering to larvae and obscuring them in the fixative solution. Serially dehydrated larvae that had been in fixative three days were rinsed in distilled water but retained a coating of precipitate. Clarity of larval external and internal morphology after 90 days in alcohol was similar to that of live specimens but had degenerated considerably when observed at 7 months. No additional body color was noted initially in larvae stored in fixative, but pigment markings disappeared. External and internal morphology were clearly distinguishable at 60 days after fixation. As previously noted, larvae stored in fixative for 90 days had become noticeably opaque, making the posterior end of the notochord difficult to distinguish. The larvae had also become brittle, and damage due to handling, including breakage and loss of finfold sections, was greater.

10% Paraformaldehyde in 0.1 M Phosphate Buffer (pH 7.4)

Effect of Fixation and Subsequent Dehydration—Little change in MNL was noted for larvae fixed in paraformaldehyde and dehydrated in 30% ethanol, but shrinkage increased approximately 6% with each subsequent alcohol change. When dehydrated in 70% ethanol, larvae had decreased in MNL by 16.74% (Fig. 1).

Effect over Time—No significant change in MNL was noted for larvae preserved in buffered paraformaldehyde for 30 days (Fig. 2), but maximum MNL shrinkage of 5.06% was observed 90 days after fixation (Table 1). The initial fixative pH was 7.4; it had not changed after 90 days.

Morphological Changes—Precipitate also formed in buffered paraformaldehyde, making it difficult to locate specimens in the vials. Pigment markings were indistinguishable in both treatment groups. There was no change in body color in animals stored in paraformaldehyde, and their

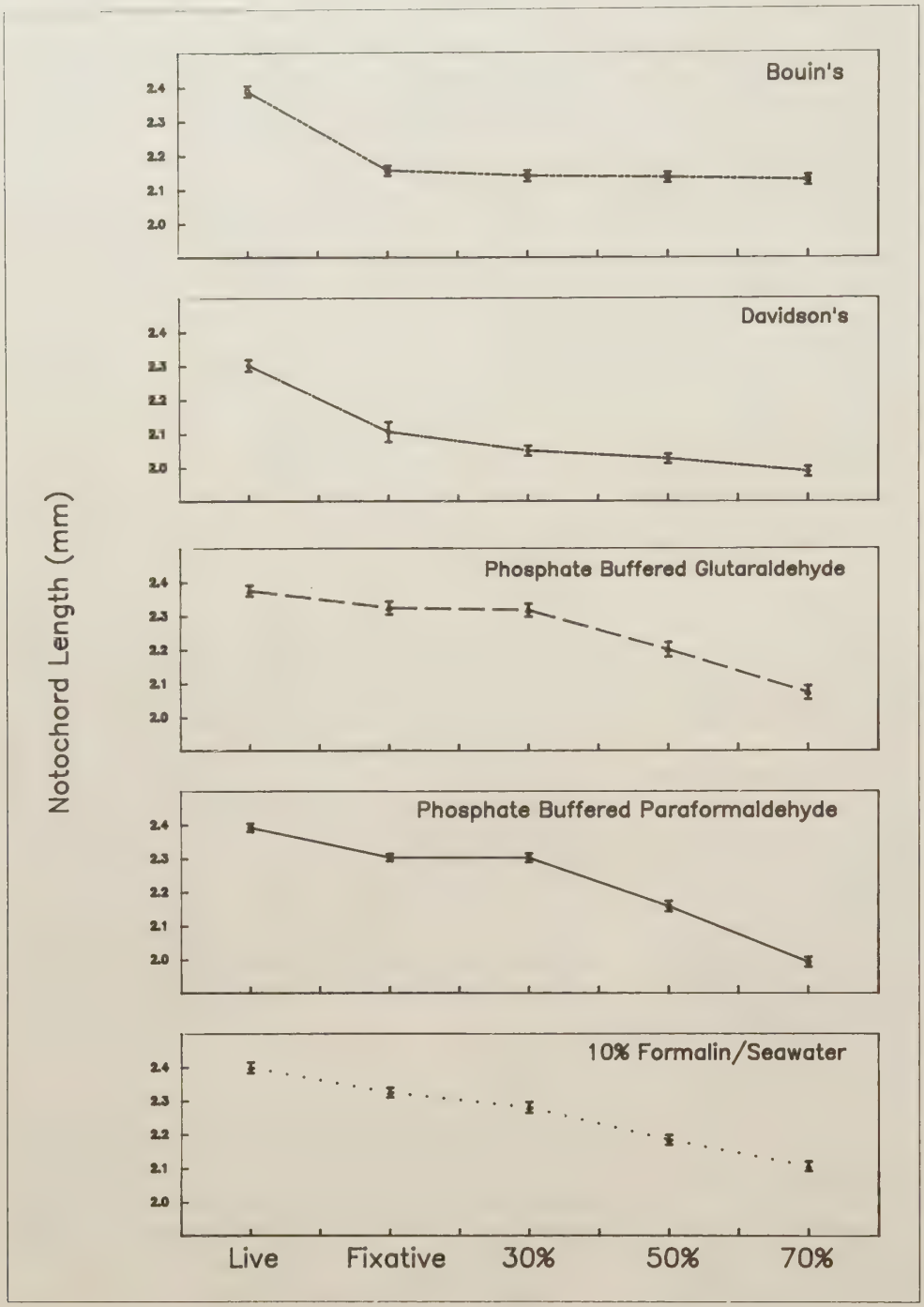

Figure 1
Group A: Effect of fixation and ethanol dehydration on changes in notochord length (mm). Error bars represent standard error.

fixed appearance was similar to that of live specimens. Dehydrated larvae turned a light brown color in alcohol, and viscera were no longer distinguishable.

10% Formalin in Seawater

Effect of Fixation and Subsequent Dehydration—Larvae fixed in formalin/seawater shrank significantly upon initial fixation. Little additional shrinkage occurred after transfer of larvae to 30% ethanol, but shrinkage increased approximately 4% when larvae were transferred to 50% ethanol and increased another 2.91% when they were transferred to 70% ethanol (Fig. 1; Table 1).

Effect over Time—Larvae stored in 10% formalin/seawater shrank significantly (4.18%) after 30 days in fixative (Fig. 2; Table 1), but little difference in MNL was observed in subsequent measurements. A total shrinkage of 5.86%

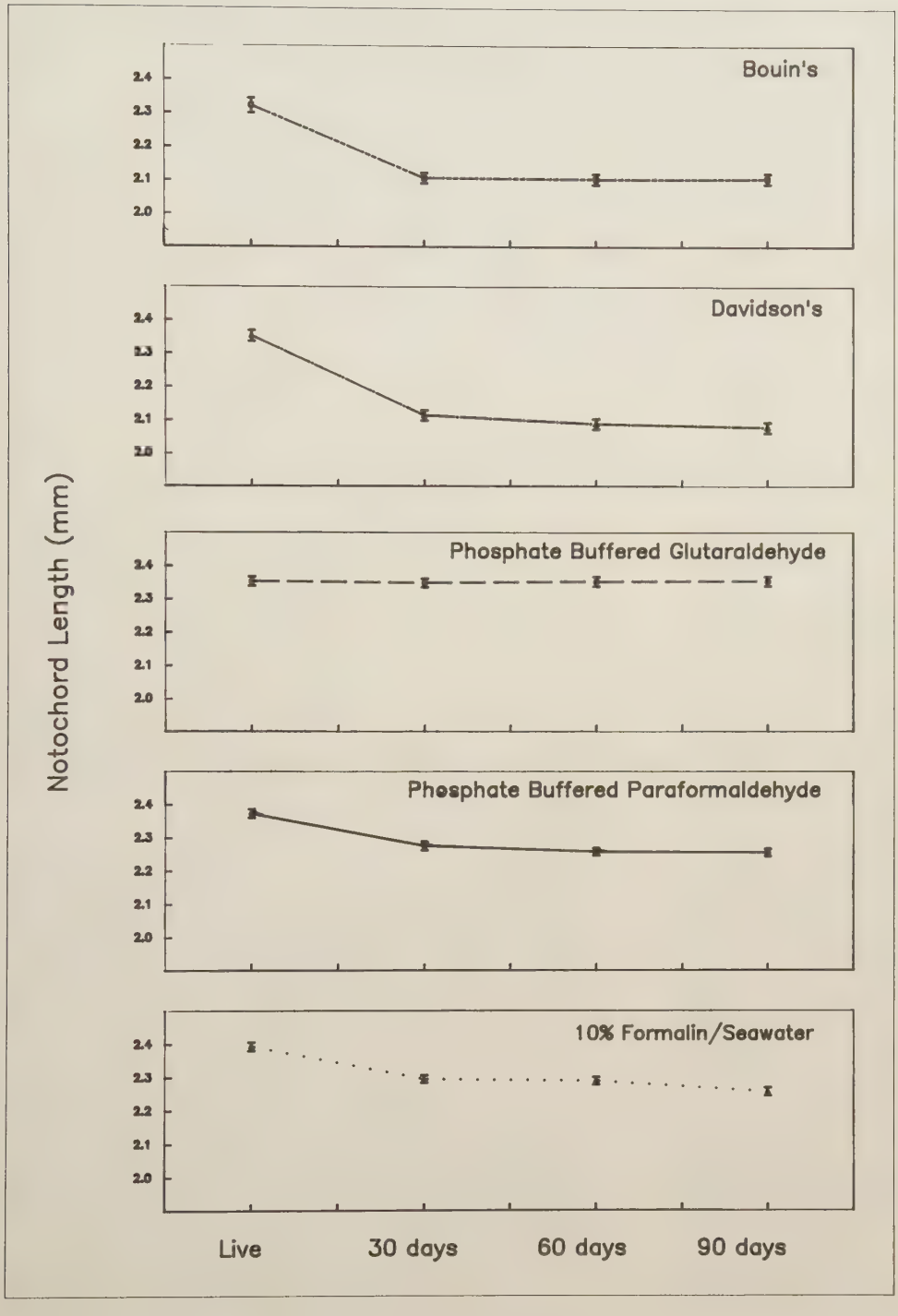

Figure 2
Group B: Effect of fixation over time on changes in notochord length (mm). Error bars represent standard error.

was recorded at 90 days. The initial fixative pH was 6.6; it had changed to 7.1 after 90 days.

Morphological Changes—Tissue clarity was reduced in larvae stored in fixative, and internal morphology became indistinguishable in dehydrated larvae. Pigment markings disappeared in both treatments, and body color changed to light brown in alcohol. A slight precipitate formed in the fixative, but larvae were not obscured.

Overall Treatment Effects

Glutaraldehyde was the only fixative that did not cause significant larval shrinkage over time (Table 2; Fig. 2). However, when followed by an ethanol dehydration series, significant shrinkage occurred (Fig. 1). All other treatments (Group B) and treatment combinations (Group A) caused significant shrinkage of larvae (Table 2).

Table 2
Overall treatment effect of fixation and ethanol dehydration (Group A) and fixation over time (Group B).

	Group A		Group B	
	F value	Significance	*F* value	Significance
Phosphate buffered paraformaldehyde	267.38	0.0001	58.45	0.0001
Phosphate buffered glutaraldehyde	138.86	0.0001	0.07	0.9756
10% Formalin/ seawater	152.10	0.0001	80.55	0.0001
Davidson's solution	161.98	0.0001	188.69	0.0001
Bouin's solution	183.25	0.0001	133.55	0.0001

Discussion

Size, as indicated by notochord or standard length, is important in the evaluation of larval growth and development. The amount of shrinkage as a result of fixation and dehydration must be considered for an accurate estimate of live parameters. Thus, the choice of fixative can play a key role in obtaining reliable growth data. However, fixative and preservative choice will depend upon the goals of the particular study, and no single fixative has been found to be ideal for all types of fixation and preservation.

Bouin's and Davidson's solutions are often used for histological analyses; Bouin's, however, can render tissues brittle. Davidson's is the preferred fixative for gonad examination. The acid component of these solutions makes them unsuitable for osteological examinations. Both solutions caused significant shrinkage in the present study, whether larvae were stored in fixative or dehydrated. Theilacker (1980) reported an 8% decrease in standard length (SL) of feeding larvae fixed in Bouin's, although shrinkage of other body dimensions ranged up to 25%. Leslie and Moore (1986) examined freshwater larvae fixed in Davidson's B and reported mixed results, with shrinkage ranging from unmeasurable for yolk-sac larvae to 4.3% for larger larvae. These investigators suggested that freshwater larvae may respond differently to fixation and that real differences in the extent of length changes may be related mainly to osmotic processes.

Larvae fixed in phosphate-buffered glutaraldehyde did not shrink significantly during either initial fixation or during storage in fixative for more than 90 days, but pigment markings disappeared. Oozeki and Hirano (1988) reported similar results for glutaraldehyde-fixed sea-bream larvae. In contrast, Stickland (1975) reported significant shrinkage of muscle fibers fixed in phosphate-buffered glutaraldehyde; he did, however, note the superior preservation of muscle tissue for histological studies. Taylor (1977) claimed that glutaraldehyde is superior to formaldehyde for fixing soft tissue because glutaraldehyde is a more efficient crosslinking agent.

Larvae stored in buffered paraformaldehyde had shrunk 3.76% at 3 days after fixation and 4.97% at 90 days, at which time tissue transparency was sufficient to allow observation of internal morphology. Dehydration to 70% ethanol resulted in shrinkage of 16.72%, the maximum of all fixatives evaluated, and also resulted in change in body color and loss of tissue transparency.

Formaldehyde solutions are by far the most common means of fixation and preservation for larval fishes and were recommended by some authors (Richards and Berry 1973; Ahlstrom 1976). Snook larvae fixed in 10% formalin/seawater had initial shrinkage of 4.13% after 30 days and a total shrinkage of 5.81% after 90 days. Shrinkage of clupeoid larvae fixed in formalin/seawater solutions varied according to the strength of the solution (Hay 1982); salinity (Hay 1982); length of time the larvae stayed in the net (Theilacker 1980; Hay 1981); and whether the larvae were field-caught or laboratory-reared (Blaxter 1971). Larvae of the southern flounder, *Paralichthys lethostima*, fixed in unbuffered and buffered 10% formalin/seawater shrank 5.2% and 7.3%, respectively, when stored in fixative and periodically evaluated over 6 years (Tucker and Chester 1984). In two size classes of freshwater fish, length increased initially following fixation in freshwater formaldehyde solutions; after 65 days in isopropyl alcohol, length approximated live length (Billy 1982).

Alcohol fixation and storage is necessary when otolith examination is desired; however, pH should be carefully monitored (Radtke and Waiwood 1980). Alcohol is still used extensively as a long-term preservative for fish larvae because it is inexpensive and does not carry the health risks of other preservatives. Nonetheless, the degree of shrinkage is greater in alcohol than it is in other fixatives. In addition, tissues become discolored and pigment mark

ings disappear. Pigment retention can be extremely important when larval indentification is required or when life-history series, sensu Moser and Ahlstrom 1970, are a research goal. It should be noted, however, that other factors such as exposure to light and fluctuating temperature may have caused the observed pigment loss.

Alcohol cannot be recommended as a preservative when health risks of alternative preservatives can be greatly reduced with mechanical ventilation of storage facilities and work areas, and safe, proper handling of potentially carcinogenic solutions. Tucker and Chester (1984) recommended 4% formalin/distilled water buffered with sodium acetate for long-term preservation and storage.

Fish larvae are collected following many different protocols. Morphological parameters such as size, chromatophore patterns, and osteology can be affected by handling, fixation, and storage methods. Evaluation of the effects of fixation and storage on morphology, as evidenced by shrinkage of animals and other morphological changes, is needed to allow critical evaluation of specimens. Choosing the best fixative for use in a study can contribute significantly to obtaining reliable results. Of the five fixatives evaluated in this study, one can not be recommended over the others based on shrinkage alone. How the preserved tissue is to be examined and/or further processed for embedding, sectioning, and staining must be considered in order to choose the most suitable fixative for the research. Different fixatives for aliquots of the same sample have been used when larvae were to be studied for more than one purpose (Oozeki et al. 1989). In the present study, phosphate-buffered glutaraldehyde caused the least amount of shrinkage, whereas live appearance was best maintained when larvae were fixed and stored in phosphate-buffered paraformaldehyde.

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Histological Effects from Long-Term Storage of Common Snook Yolk-Sac Larvae in Fixatives and Alcohol

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ABSTRACT

Yolk-sac larvae were fixed in five fluids (Bouin's fluid, Davidson's fluid, 3% glutaraldehyde in 0.1 M phosphate buffer, 10% paraformaldehyde in 0.1 M phosphate buffer, and 10% formalin/seawater) and stored for more than two years in fixative or 70% ethanol. All larvae were dehydrated in 95% ethanol, infiltrated, and embedded in glycol methacrylate resin. Sagittal sections cut at 3.5 μm were stained with hematoxylin and eosin or periodic acid/Schiff's stain and evaluated for quality of histological results and possible presence of artifacts. Aldehydes provided optimum fixation for histological evaluation, but the best fluid for long-term storage depended upon the aldehyde used.

Introduction

Histological evaluation has been used to determine the nutritional status of field-caught fish larvae through morphometric evaluation of various structures (Ehrlich et al. 1976; Theilacker 1978), gross condition of various tissues and structures (O'Connell 1976; 1980), and histological indication of active absorption of proteins (Oozeki et al. 1989). Although various fixatives have been used, the discussion of tissue appearance has usually not included possible fixation artifacts even though observations of shrinkage (Hay 1982; Tucker and Chester 1984; DeLeon et al. 1991) and loss of pigments (Ahlstrom 1976) have demonstrated that artifactual changes occur. Further, histological investigations of larval fish tissues have, with few exceptions (Govoni 1980), relied on evaluation of tissues subjected to paraffin embedment, a process that causes substantial shrinkage (Ross 1953; Baker 1958).

In the past, the requirements of paraffin embedment have dictated the use of fixatives containing coagulative chemicals (Baker 1958). Noncoagulative aldehyde fixatives have long been recognized as best for tissues examined by electron microscopy (Glauert 1978). However, most plastics that are stable under the electron beam are water insoluble and not compatible with the majority of histological stains, which are soluble only in water. Introduction of a water-soluble plastic embedding resin, glycol methacrylate, has allowed greater use of aldehyde fixatives for light microscopy. No previous studies have specifically compared the effects of different primary and combination fixatives on the histology of larval fishes. This paper addresses the effects of commonly used tissue fixatives and preservatives on laboratory-spawned yolk-sac larvae of the common snook (*Centropomus undecimalis*) embedded in glycol methacrylate.

Materials and Methods

Four hundred common snook larvae hatched from laboratory-spawned eggs were collected live 18–24 hours after hatching and were placed individually in vials containing approximately 1 mL of fixative. Five fixatives were evaluated: Bouin's fluid (Sheehan and Hrapchak 1980); Davidson's fluid (Yevich and Barszcz 1977); 3% glutaraldehyde in 0.1 M phosphate buffer; 10% paraformaldehyde in 0.1 M phosphate buffer; and 10% formalin in seawater (formalin/seawater). The total sample was divided into groups A and B. Each group was composed of 5 subgroups of 40 individuals, each representing one of the five fixatives. After 3 days in fixative, Group A was serially dehydrated to 70% ethanol. Group B samples remained in fixative. Both groups were then stored at room temperature on open shelves under normal laboratory lighting for 31 months.

Six larvae from each fixative treatment in groups A and B were dehydrated to 95% ethanol and embedded in glycol

Table 1

Summary of quality of fixation and preservation of various tissues and structures. P = poor, A = acceptable, E = excellent, (+) = observed, (−) = not observed, FAP = fixed and preserved, H&E = hematoxylin and eosin.

	Digestive tract	Muscle tissue	Brain & nerve cord	Nuclear morphology	Pituitary	Eye	Otoliths	Finfold	H&E stain
Bouin's w/ ethanol	A	P	P	P	P	P	(−)	P	P
Bouin's F&P	P	P-A	P	P	P	P	(−)	P	P
Davidson' w/ ethanol	A	P-A	P	P	P	P	(+)	P	P
Davidson's F&P	P	A	P	P	P	P	(+)	P	P
10% formalin/seawater w/ ethanol	P	P	P	P	P	P	(+)	P	E
10% formalin/seawater F&P	P-A	P	P	P	P-A	A	(−)	P	A
Phosphate buffered paraformaldehyde w/ ethanol	A	P-A	A	A	P-A	P-A	(+)	P	E
Phosphate buffered paraformaldehyde F&P	E	E	E	A	E	E	(−)	A	E
Phosphate buffered glutaraldehyde w/ ethanol	E	A	E	A	E	E	(+)	E	E
Phosphate buffered glutaraldehyde F&P	A	E	P-A	P	P-A	A-E	(−)	E	A

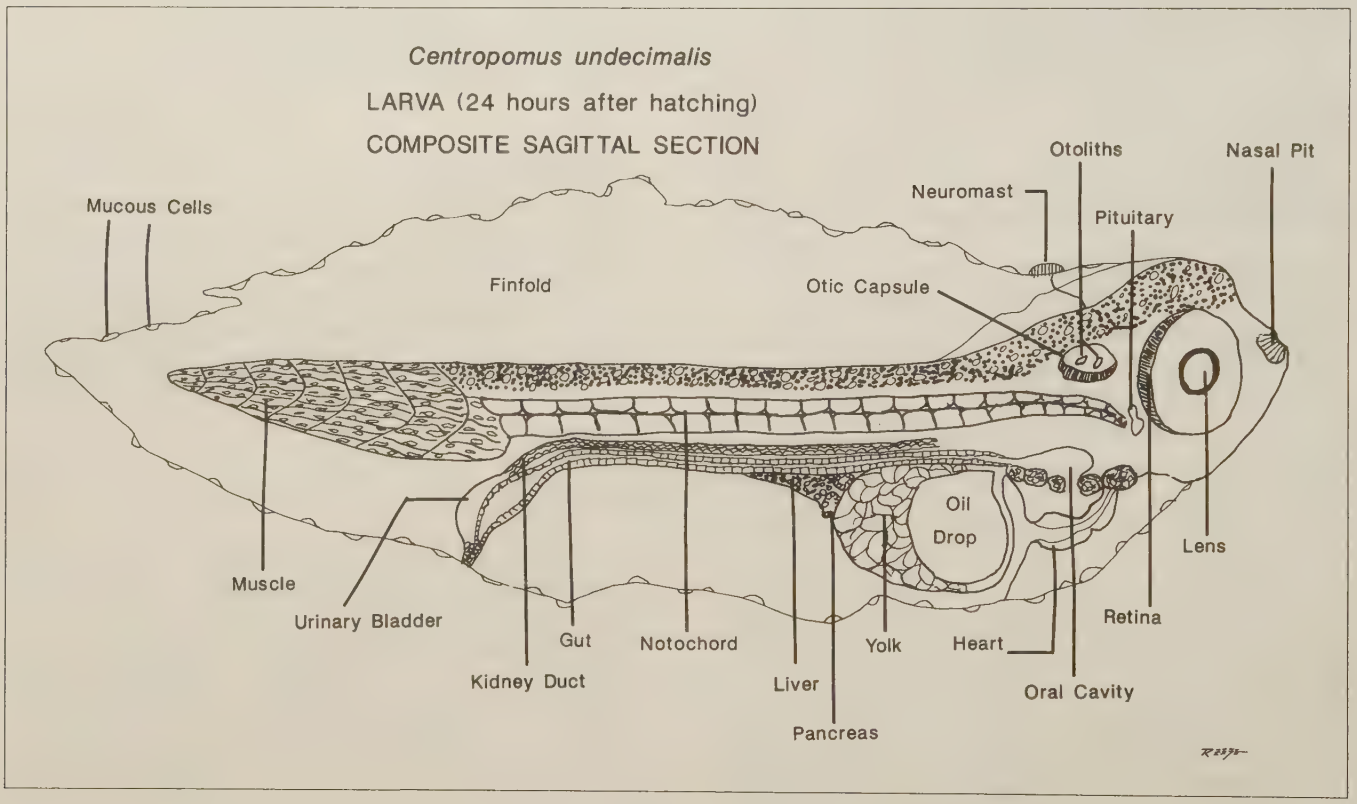


Figure 1

Composite sagittal section of a *C. undecimalis* larva 24 hours after hatching.

methacrylate (JB-4 Kit, Polysciences™*) in BEEM™* capsules. Larvae were serially sectioned in the sagittal plane at 3.5 μm with glass knives using an LKB 2218 Historange™* microtome. Sections were placed on acid-cleaned slides, baked overnight at 75°C, and stained as a group with hematoxylin and eosin (H&E) or Quintero's modified periodic acid/Schiff's stain (QPAS), which uses

* The use of commercial products does not imply endorsement by Florida Department of Natural Resources.

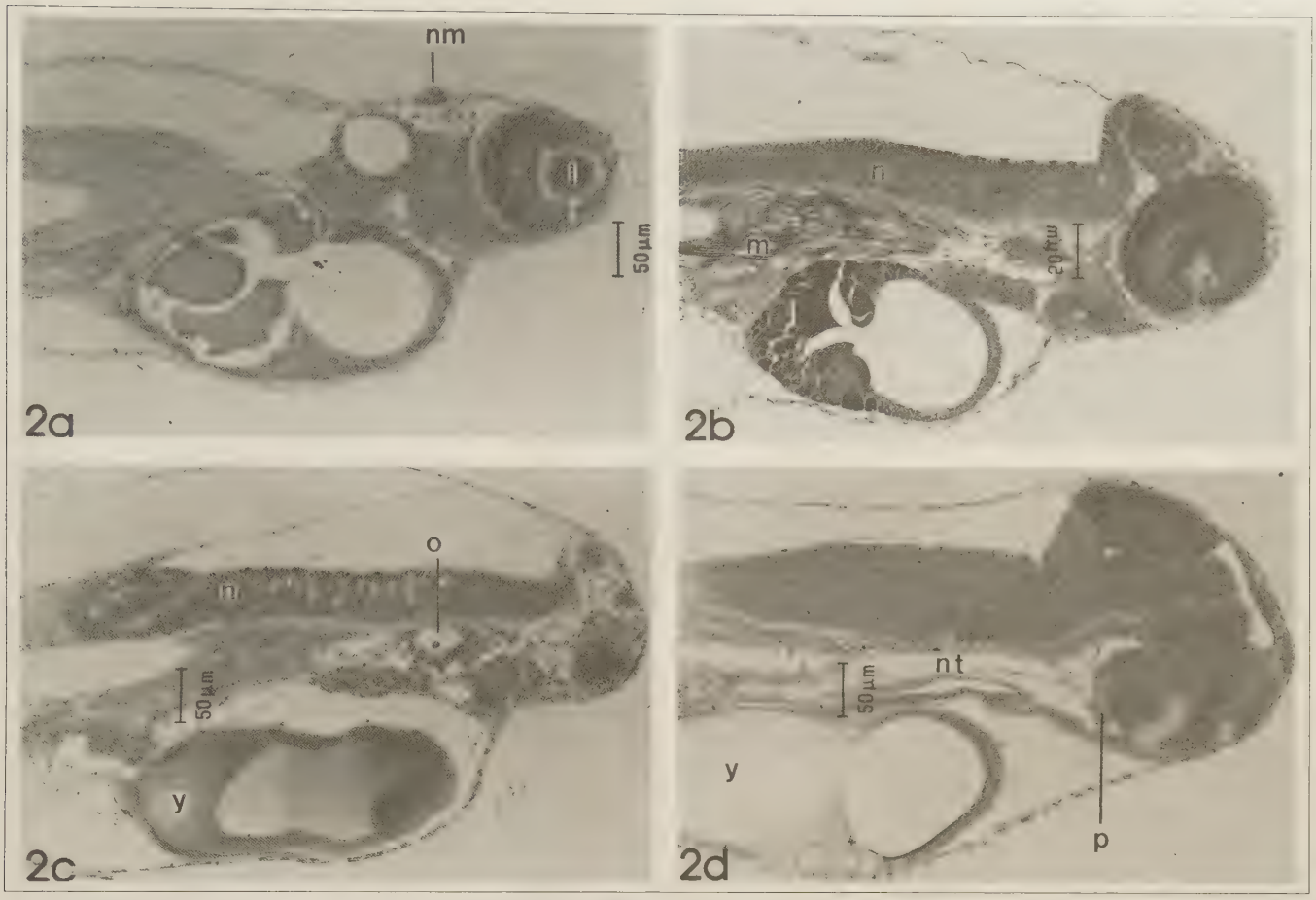


Figure 2

Midsagittal sections of *C. undecimalis* larvae 24 hours after hatching fixed in Bouin's and Davidson's fluids and stored therein or in 70% ethanol; stained with H&E. (**a**) Bouin's - stored in 70% ethanol; (**b**) Bouin's - stored in fixative; (**c**) Davidson's - stored in 70% ethanol; (**d**) Davidson's - stored in fixative. l = lens; m = muscle; nm = neuromast; n = nerve cord; nt = notochord; o = otolith; p = pituitary; y = yolk.

a counterstain of metanil yellow (Iliana Quintero, Florida Marine Res. Inst., unpubl. manuscr.).

Results

Each of the combined fixation and preservation treatments was graded as poor, acceptable, or excellent in terms of its effect on the histological clarity of features that are present in snook yolk-sac larvae (Table 1; Fig. 1). Even at low magnification (× 50), overall differences were evident.

The quality of tissues fixed in Bouin's, whether preserved in fixative or ethanol, was poor (Table 1). The material fixed in Bouin's fluid and preserved in ethanol (Fig. 2a) revealed little tissue contrast with H&E stain, and basophilia is absent in tissue stored in fixative (Fig. 2b). Tissues fixed and preserved in Bouin's fluid exhibited variable results; e.g., some tissues showed cellular swelling, whereas others were shrunken.

Tissues fixed in Davidson's fluid were of only slightly better quality (Table 1). Yolk was more confluent in appearance (Fig. 2, c and d) than with other fixatives. Staining lacked contrast, especially in the tissue stored in alcohol (Fig. 2c), which almost totally lacked eosinophilia.

Tissues fixed in formalin/seawater and preserved in alcohol shrank substantially, thereby distorting many features (Fig. 3a). However, formalin/seawater fixation with preservation in the fixative resulted in clearer histology than either Bouin's or Davidson's (Fig. 3b) and yielded better stain contrast. Overall, this fixative resulted in poor to acceptable tissues (Table 1).

Alcohol preservation of buffered paraformaldehyde-fixed tissue resulted in preparations that were of slightly better quality than formalin/seawater-fixed tissues (Fig. 3c; Table 1). Paraformaldehyde fixation with storage of tissue in the fixative, however, allowed clear identification of many features characteristic of yolk-sac snook larvae (Table 1; Fig. 3d). Stain contrast was sharp. The globular shape of

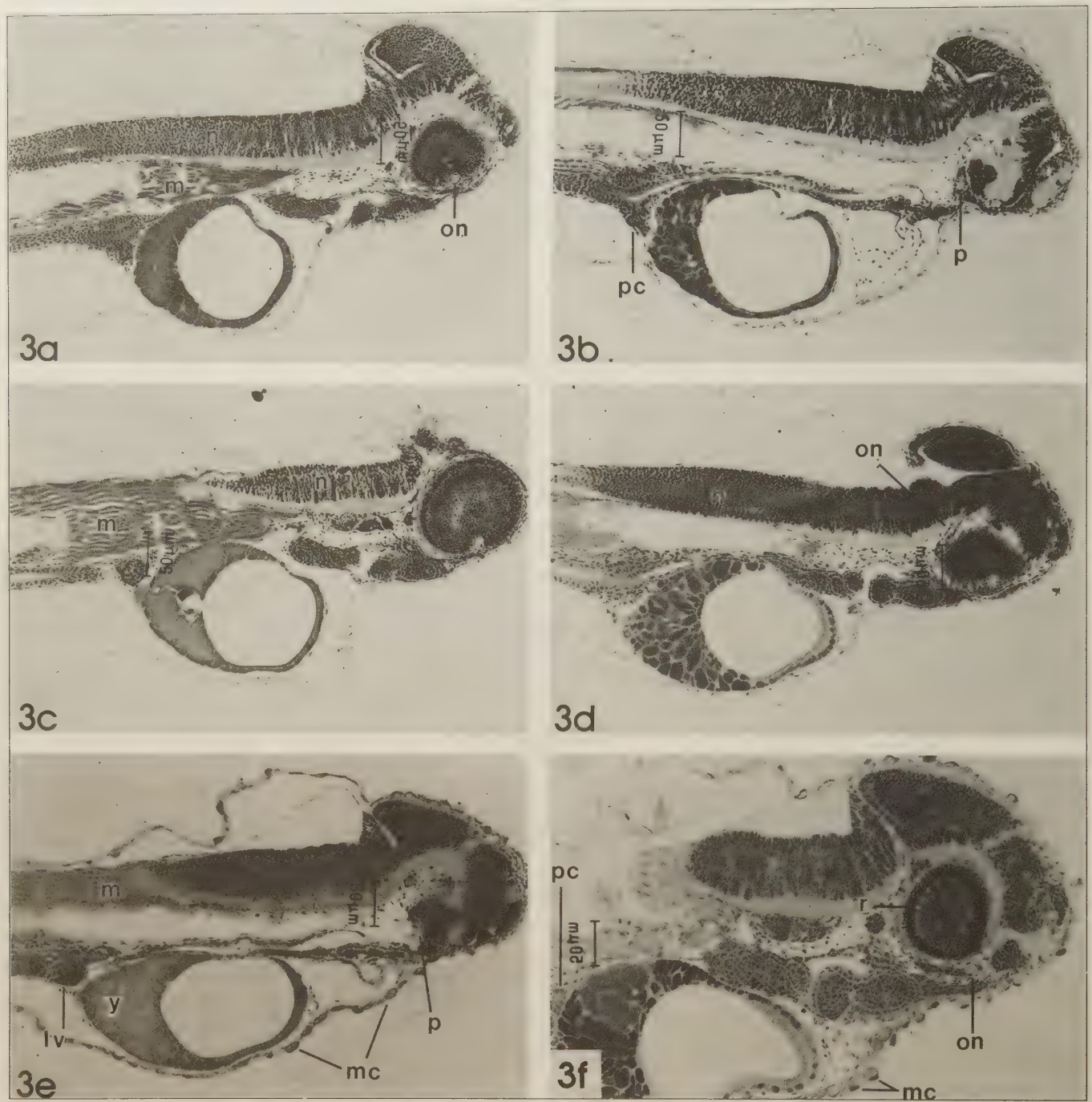


Figure 3

Midsagittal sections of *C. undecimalis* larvae 24 hours after hatching fixed in aldehydes and stored therein or in 70% ethanol; stained with H&E. (**a**) Formalin/seawater - stored in 70% ethanol; (**b**) Formalin/seawater - stored in fixative; (**c**) Paraformaldehyde in phosphate buffer - stored in 70% ethanol; (**d**) Paraformaldehyde in phosphate buffer - stored in fixative; (**e**) Glutaraldehyde in phosphate buffer - stored in 70% ethanol; (**f**) Glutaraldehyde in phosphate buffer - stored in fixative. lv = liver; m = muscle; mc = mucous cell; n = nerve cord; on = optic nerve; p = pituitary; pc = pancreas; r = retina.

the finfold mucous cells was obvious, muscle fibers exhibited minimum shrinkage, and mitotic figures were clear.

Tissues fixed in phosphate-buffered glutaraldehyde and preserved in ethanol (Table 1; Fig. 3e) provided better structural delineation than any other treatment. Preservation in glutaraldehyde (Fig. 3f) achieved similar fixation quality, but the tissue was brittle and difficult to handle without fracture. Stain contrast was acceptable, but not

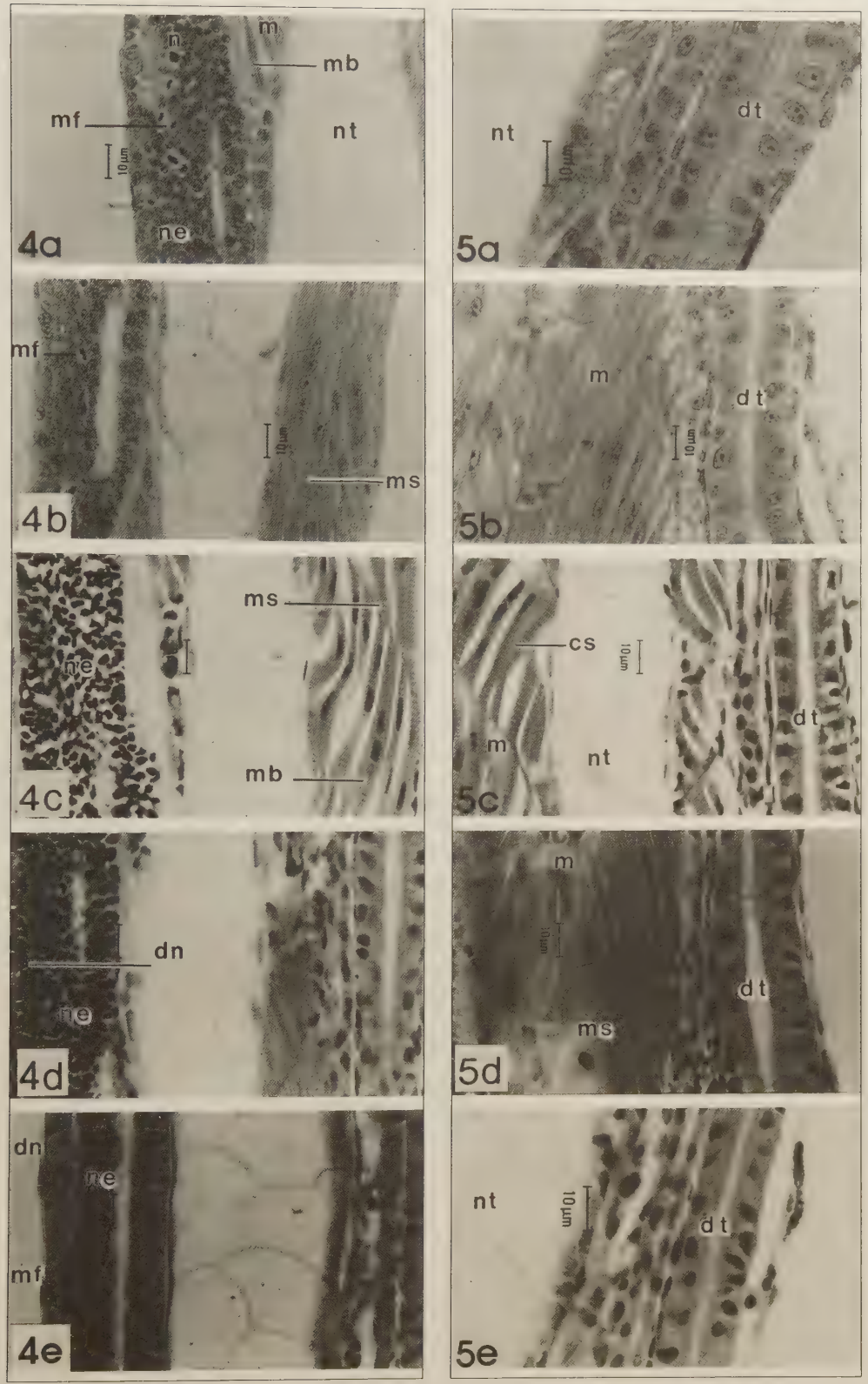


Figure 4
Midsagittal sections through nerve cord and notochord of *C. undecimalis* larvae 24 hours after hatching; (**a–d**) stained with H&E; (**e**) stained with PAS/metanil yellow. All sections aligned similarly to show tissue comparisons.

Figure 5
Midsagittal sections through digestive tube of *C. undecimalis* larvae 24 hours after hatching; stained with H&E. All sections aligned similarly to show tissue comparisons.

(**a**) Bouin's - stored in 70% ethanol; (**b**) Davidson's - stored in 70% ethanol; (**c**) Formalin/seawater - stored in fixative; (**d**) Paraformaldehyde - stored in fixative; (**e**) Glutaraldehyde - stored in 70% ethanol. cs = cross striations; dn = differentiating neuron; dt = digestive tract; m = muscle; mb = myofiber; mf = mitotic figure; ms = myosepta; n = nerve cord; ne = neuroepithelium; nt = notochord.

as well defined as with other aldehyde preparations (Table 1).

Examination of tissue at higher magnification (× 330) revealed more detailed differences among treatments. For example, in neural tissue, small neuroepithelial cells with dark basophilic nuclei appeared in all treatments (Fig. 4). Cells with large, round, lightly basophilic nuclei and a single nucleolus, representing differentiating neurons, were

most clearly seen in tissue fixed with paraformaldehyde or glutaraldehyde (Fig. 4, d and e). In contrast, poor fixation resulted in nerve cord shrinkage (Figs. 2c; 3, a and c), which grossly distorted the appearance of individual cells.

Fixation of the digestive tract was adequate in most fixative/ preservative combinations (Table 1). In tissues fixed in Bouin's and Davidson's fluids, clumped mitotic figures were abundant and nuclei were centrally located within swollen cells with coagulated cytoplasm (Fig. 5, a and b). Preservation of formalin/seawater-fixed tissue in alcohol produced substantial shrinkage and pycnotic nuclei (Fig. 5c). In paraformaldehyde- and glutaraldehyde-fixed tissue (Fig. 5, d and e), nuclei were in the proximal third of the cuboidal cell, and the homogeneous cytoplasm revealed no evidence of inclusions. Only a small liver primordium was present, posterior and lateral to the yolk (Fig. 3e). Liver mitotic figures were clear in the aldehyde fixatives. Two to three exocrine pancreatic acini were obvious in all larvae fixed in aldehydes (Fig. 3, b and f).

In paraformaldehyde- and glutaraldehyde-fixed larvae, the chevron-shaped segmented myomeres consisted of confluent myofibers with multiple, oval, centrally located nuclei with a single nucleolus (Fig. 6) and well-defined myosepta. Shrinkage was minimal, but the cross striations (A and I bands) were not sharp. In tissues fixed in Bouin's, Davidson's, and formalin/seawater, the muscle fibers were shrunken and separated and myosepta were not clear (Fig. 4, a through c). However, cross striations (Fig. 5c) were well defined.

Most nuclei in developing snook larvae were basophilic and processed granular chromatin, which is typical of interphase. In some nuclei, single or multiple nucleoli were visible. In Bouin's and Davidson's fixatives, all nuclei had peripherally clumped chromatin with a central body resembling a nucleolus. This chromatin clumping also interfered with the observation of mitotic stages (Fig. 4, a and b). The preservation of mitotic figures was superior in glutaraldehyde-fixed tissue (Fig. 7).

In tissues fixed in glutaraldehyde, the differentiating lens fibers of the eye were fully nucleated and minimally shrunken. The retinal layer was clearly defined and its basal area contained many mitotic figures, but no pigment was observed (Fig. 8). In aldehyde-fixed tissue, the large optic nerve with its sheathing cells (Fig. 3 a, d, and f) could be followed from the choroid fissure to the contralateral side of the brain, where it terminates in the diencephalon (Fig. 3d). In poorly fixed tissues, the differentiated areas of the eye were less obvious, the retinal structure was unclear, the optic nerve was not visible, and the lens was severely shrunken (Fig. 2a).

In the otic capsule, two of the three otolith pairs, probably sagittae and lapilli, were visible when fixed in glutaraldehyde and preserved in ethanol (Fig. 9). Otoliths were present, but not optimally fixed, in all animals fixed in aldehydes and preserved in alcohol and in all larvae fixed in Davidson's, whether preserved in alcohol or fixative (Table 1; Fig. 2c).

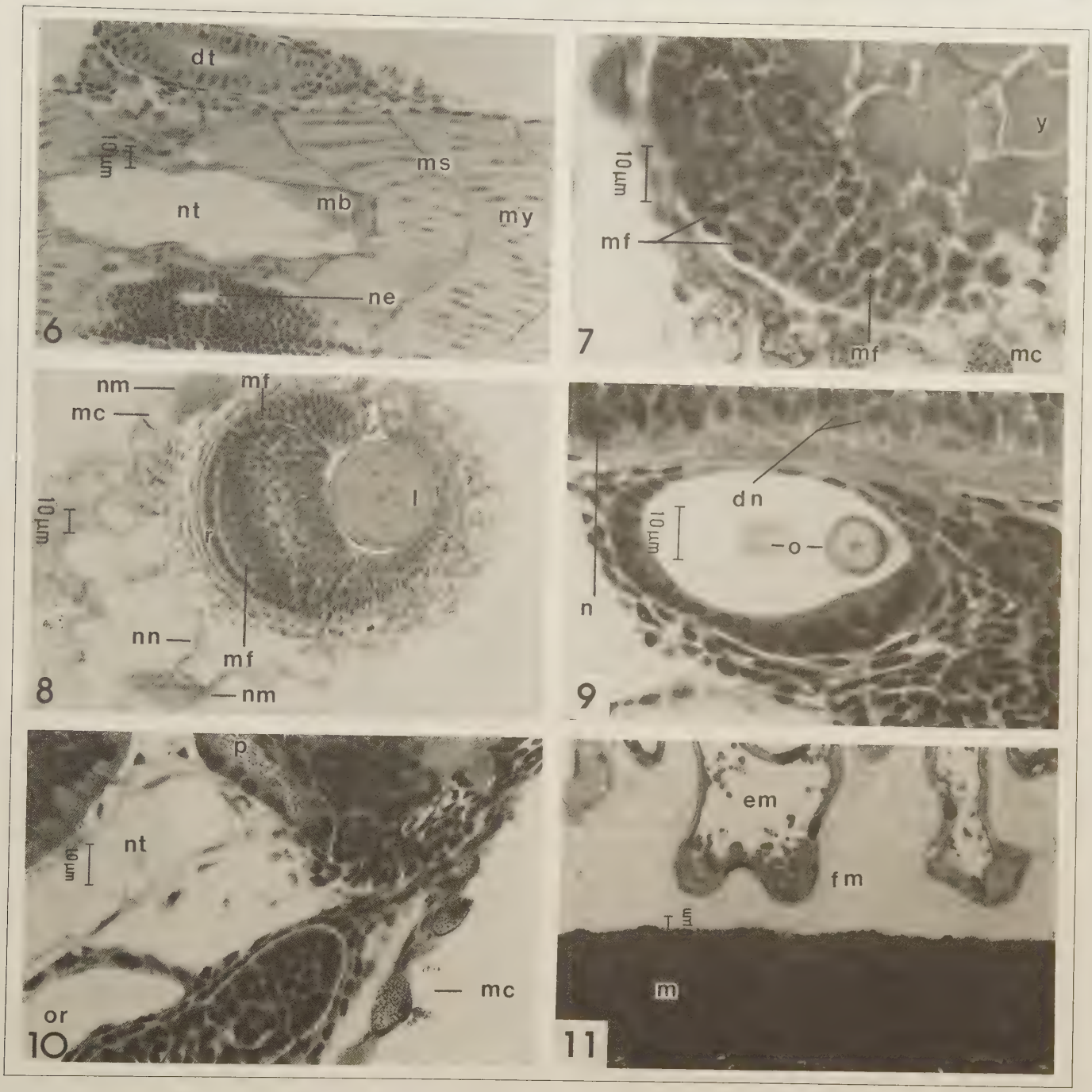
Structural definition of the lobular pituitary, anterior to the tip of the notochord, was best in aldehydes (Figs. 3, b and e; and 10). In Davidson's- and Bouin's-fixed tissues, a separate pituitary structure was not well defined (Fig. 2d).

The finfold is composed of a two-layered epithelium with many mucous cells subtended by an acellular matrix. Not evident in most fixed sections, however, is a dense fibrillar material seen in larval tissue that has been fixed and preserved in glutaraldehyde and stained with QPAS (Fig. 11). Hematoxylin staining of the same tissue was unremarkable (Fig. 2f). In glutaraldehyde-fixed material, the mucous cells were spherical and their basal nuclei and granular contents were well defined (Figs. 3, e and f; 7; 8; and 10). In poorly fixed tissue, the finfold epithelium appeared as a thin filamentous structure with a few poorly defined cells (Fig. 2). Many neuromasts were present along the finfold epithelium in all preparations, but structural detail was variable (Figs. 2a and 8). Nerve tracks subtending peripheral neuromasts were seen only in glutaraldehyde-fixed tissues (Fig. 8).

Discussion

In general, chemical fixatives are either coagulant or noncoagulant. A specific chemical may be preferred for preservation of a particular tissue or structure or to aid in diagnostic staining. However, some chemicals may have a negative impact on tissues, causing swelling, shrinkage, or other types of cellular distortion. Therefore, primary chemical fixatives are often combined in an attempt to balance the defects of one primary fixative by adding another fixative with compensating properties. For example, two of the most commonly recommended fixative mixtures for histological examination of teleost tissues are Bouin's and Davidson's solutions. In Bouin's fluid, picric acid, a coagulant fixative that facilitates the admission of paraffin by tissues, also shrinks tissue and renders chromatin acidophilic. Acetic acid, a noncoagulant component, is used to compensate for picric acid. However, acetic acid swells protein gels and fibers and produces a precipitate with nucleoprotein. The formaldehyde in Bouin's fixes cytoplasm well, defines chromosomes poorly, and hinders the penetration of paraffin into tissues (Baker 1958).

The lack of basophilia in tissues preserved for over two years in Bouin's was not surprising, because fluids intended only for rapid fixation, such as Bouin's and other coagulative mixtures, invariably lead to excessive hardening (Steedman 1976). Retention in such fixatives is not normally recommended, but was included here as part of an overall comparison.



Figures 6–11

6. Myomere of *C. undecimalis* larva 24 hours after hatching, fixed in paraformaldehyde and stored in fixative; H&E stain. dt = digestive tract; mb = myofiber; ms = myosepta; my = myomere; ne = neuro-epithelial cell; nt = notochord.
7. Mitotic figures in liver of *C. undecimalis* larva 24 hours after hatching, fixed in glutaraldehyde and stored in ethanol; H&E stain. mc - mucous cell; mf = mitotic figure; y = yolk.
8. Eye and neuromast of *C. undecimalis* larva 24 hours after hatching fixed in glutaraldehyde and stored in alcohol; PAS/metanil yellow stain. l = lens; mc = mucous cell; mf = mitotic figure; nm = neuromast; nn = neuromast nerve; r = retina.
9. Otic capsule and otolith of *C. undecimalis* larva 24 hours after hatching fixed in glutaraldehyde and stored in alcohol; H&E stain. dn = differentiating neuron; n = nerve cord; o = otolith.
10. Pituitary, tip of notochord, and edge of finfold with mucous cells of *C. undecimalis* larva 24 hours after hatching fixed in glutaraldehyde and stored in alcohol; H&E stain. mc = mucous cell; nt = notochord; or = oral cavity; p = pituitary.
11. Muscle and finfold of *C. undecimalis* larva 24 hours after hatching fixed in glutaraldehyde and stored in fixative; PAS/metanil yellow stain. em = external milieu; fm = finfold matrix; m = muscle.

Davidson's fluid consists of the noncoagulant fixatives acetic acid and formaldehyde combined with the coagulant fixative ethanol. In addition to the previously mentioned effects of acetic acid and formaldehyde, ethanol denatures protein, precipitates nucleic acids without rendering them insoluble in water (Baker 1958), and shrinks and hardens tissues. Glycerol, which is not a fixative, was added to this combination as a softening agent, enhancing fixation results (Hinton et al. 1984).

The most widely used noncoagulant fixatives are aldehydes, principally formaldehyde and glutaraldehyde. The distinction between formalin and formaldehyde is often not clearly defined. Commercial formalin consists of 37–41% formaldehyde dissolved in water containing many trace elements and 7–13% methanol, which is added to prevent polymerization (Steedman 1976). Paraformaldehyde is a polymer that can be prepared to yield a pure, relatively stable, aqueous formaldehyde without additives. The cross-link bonds of this monoaldehyde are not as stable as those of glutaraldehyde, and soaking tissues in water can remove many of the cross-linking bonds, thus destroying some of the valuable effects of formalin fixation (Stickland 1975). Glutaraldehyde is a dialdehyde and stabilizes structures by cross-linking before cellular contents are extracted (Glauert 1978). Tissue fixation in glutaraldehyde results in better structural retention and slightly less shrinkage than in formaldehyde (Stickland 1975). Long-term storage in buffered glutaraldehyde caused tissue to be brittle and difficult to handle without fracture. This dialdehyde produces strong cross-links between protein molecules and results in a progressively growing reticulum inside the cell (Geyer 1973). This continued cross-linking may cause the brittle tissue condition noted with long-term storage in glutaraldehyde. The presence of extensive aldehyde groups is also suggested by intensified staining with QPAS, which links through aldehydes (Sheehan and Hrapchak 1980). The finfold matrix, not normally evident in fixed sections, appeared in QPAS-stained material of glutaraldehyde-fixed and stored larvae as a dense fibrillar matrix. Muscle tissue also showed clumping of stain.

In the present study, three variations of aldehyde fixation were evaluated: commercial formalin buffered with seawater, commonly used for life-history studies; paraformaldehyde buffered with phosphate, the fixative of choice for histological preparation in many laboratories; and glutaraldehyde buffered with phosphate, a fixative introduced in 1963 for electron microscopy (Sabatini et al. 1963) that has also been used successfully with a variety of teleost tissues (Watanabe 1981; Kessel et al. 1985). Only recently has glutaraldehyde been used for ichthyoplankton preservation (Oozeki and Hirano 1988). Glutaraldehyde fixation causes tissues to become hard during paraffin embedding. Differences in hardness between the paraffin embedding medium and the processed tissue causes tissue fracture during sectioning. The hard plastic embedding media used for electron microscopy infiltrate glutaraldehyde-fixed tissue well and allow thin sectioning without fracture.

In the past, the requirements of paraffin embedding have, to a large extent, controlled the choice of fixatives. However, Baker (1958) speculated that the introduction of new embedding media was likely to result in less reliance on coagulative fixatives. Water-insoluble plastic embedding media are used for electron microscopy. Because the spectrum of histological stains comprises mostly water-soluble pigments, the tinctorial choices for tissues embedded in these early resins were greatly reduced. Introduction of glycol methacrylate, a water-soluble resin, not only provided a harder substrate easily sectioned at 2 μm but also was expected to allow the use and/or adaptation of diagnostic stains developed for paraffin. Although few diagnostic stains available for paraffin preparations have been successfully adapted for use with glycol methacrylate-embedded tissues, some stain combinations have proved suitable (Govoni 1983). For this investigation, a modified H&E stain and PAS technique using metanil yellow as a counterstain, which yields excellent histological detail (Quintero, in prep.), were used. In addition, infiltration and embedment in glycol methacrylate can be accomplished at relatively low temperatures rather than the 55–65°C required for paraffin, thus reducing the degree of temperature-induced hardening and artifact.

The best histological results were achieved with fixation in the two pure buffered aldehydes, but the best preservative depended upon the aldehyde used. Fixation in glutaraldehyde and subsequent preservation in ethanol were superior for most tissues. Nerve tracks subtending peripheral neuromasts (Fig. 8) were seen only in glutaraldehyde-fixed tissue; perhaps greater initial shrinkage in other fixative fluids (DeLeon et al. 1991) caused a separation of these fine nerves. Fixation in phosphate-buffered paraformaldehyde with subsequent preservation in the fixative also resulted in generally excellent histology.

Hopwood (1969) stated, "No one fixative is ideal for all situations." Careful selection of fixative is critical in the development of protocols for evaluation of teleost tissues. For example, the tissue may be prepared for examination of external features, histological evaluation requiring histochemical techniques or the application of other special research methodologies. In clinical situations, multiple fixation procedures are often used to provide for contingencies. For human surgical biopsies, Dawson (1973) recommended that samples be divided into three pieces: one to be fixed for standard paraffin embedding and subsequent histological staining, a second to be quenched (rapidly frozen below −70°C), and a third to be fixed in aldehyde for later examination using electron microscopy. Fisheries work seldom allows the luxury of such a complete initial preparation. The immediate processing and embedment of collected tissues is often impossible. Therefore, not only

should the fixation method be carefully evaluated, but additional consideration should be given to the choice of storage fluid because the preservative also has a significant effect on tissue quality. Whatever fixative technique is employed, researchers must be aware that the ultimate goal of histological fixation of tissues is not simply to avoid decay but also to clarify understanding of ongoing processes by obtaining a sample of "frozen physiology."

Acknowledgments

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